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SELECTIVE ABSORPTION OF STARLIGHT BY INTERSTELLAR CLOUDS

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Evidence of the selective absorption of starlight by nebulous material was obtained by Seares and Hubble[1] in 1920. Measures of the colors of about fifty nebulous stars (normal stars surrounded by luminous nebulosity concentrated about the stars) showed practically all the stars to be redder than would be expected from estimates of color based on their spectral types. The simplest explanation of the observed excess of color appeared to be a differential scattering of the starlight in its passage through the surrounding nebulosity.

A continuation of the observations in 1921 confirmed the earlier measures and extended the list of objects showing color-excess. A case of special interest was found near *o* Persei where a group of seventeen stars gave an average color-excess of more than 0.6 mag. and several individual values amounting to about 0.9 mag.[2] Most of these stars are imbedded in the luminous nebula IC 1985. A few, however, show no trace of surrounding luminosity but apparently are involved in the dark obscuring cloud which fills the region and depresses the star density far below normal. These instances of color-excess associated with stars in dark nebulosity gave added weight to the hypothesis of scattering as an explanation of the abnormal colors.

During the last six years numerous observers have extended and generalized these early results. Especially noteworthy are the investigations of open galactic clusters by Trumpler,[3] of globular clusters by Stebbins,[4] and of B-type stars by Stebbins and Huffer.[5] All these results show clearly that selective absorption, apart from any general absorption that may also be present, is a phenomenon of importance in questions relating to the structure of the stellar system. Quantitatively the absorption is sufficient to require a radical change in the estimated dimensions of the system. In general it is greatest close to the central line of the Milky Way, where the maximum effect would be expected on account of the number

and density of the obscuring clouds. Although statistically correct, there are many exceptions to this general statement, and, considered in detail, the phenomenon presents itself as one of the utmost complexity.

Absorption of some kind certainly occurs whenever an obscuring cloud is present, but it is by no means assured that a star involved in such a cloud will show selective absorption, for, as probably all observers have found, stars of normal color often occur within the boundaries of obscured regions. An easy explanation of the absence of selective absorption in such cases is that the stars are in front of the cloud; and in many instances this explanation is doubtless correct.

It is noteworthy, however, that early Mount Wilson observations of considerable groups of stars in certain heavily obscured regions showed normal colors for all the stars, even the faintest measured.[6] If we are to suppose that all these normal stars are in front of the cloud, the cloud itself must be sharply bounded and of such opacity that all stars within it are too faint to be recorded with the exposures used. An alternative explanation is that some of the stars observed are really within the cloud, but that the size of the particles of which the cloud is composed is mainly such that scattering is inappreciable or does not occur at all, and that only general absorption is operative.

At the other observational extreme is the case of Selected Area 40, midway between α Cygni and the North America Nebula, for which results were published in 1931.[7] The field, rich in stars, is just on the border of a region of complex obscuration. A large color-excess of about 0.8 mag.[8] affects all but a small fraction of the 760 stars whose colors have been measured. The exceptions seem to be mainly brighter objects, to some extent localized within the field, and may well be in front of the cloud. Here again general absorption may also be involved.

The results now presented relate to the colors of groups of stars, mostly between photographic magnitudes 10 and 13.5, in thirty of the Selected Areas of Kapteyn covering a wide range in galactic latitude. Color indices obtained by comparing photographic and photovisual magnitudes, all on the international system, were plotted for each field against the spectral types of Humason,[9] Schwassmann,[10] and Maxwell.[11] A superposed tracing of the standard curve connecting color-index and spectrum was then shifted parallel to the color axis until the plotted points were best represented by the curve. The displacement of the curve from its normal position then gave directly the value of the mean color-excess for the stars in question. For a group of normal color the displacement is of course zero or negligibly small.

The results for 42 groups of stars are shown in the accompanying table—19 normal in color and 23 with a color-excess which in all cases seems to be above the limit of permissible error and in the mean equal to about 0.5

mag. Ten additional groups not included in the table (99 stars in Areas 2, 8, 10, 18, 40, 61, 65, 73, 85 and 108) also show an excess of color, which in the main must also be real, with a mean of 0.23 mag. Twelve of the 23 areas showing color-excess also include groups of stars which are normal in color.

The fifth column of each division of the table indicates the inference as to obscuration drawn from Hubble's counts of extra-galactic nebulae.[12] All but three of the groups of normal color occur in regions of normal (*N*) nebular density. Groups showing color-excess, on the other hand, are

TESTS FOR SELECTIVE ABSORPTION

STARS OF NORMAL COLOR					STARS SHOWING COLOR EXCESS				
SELECTED AREA	GALACTIC LATITUDE	COLOR-EXCESS	NO. STARS	OBSCURATION†	SELECTED AREA	GALACTIC LATITUDE	COLOR-EXCESS	NO. STARS	OBSCURATION†
3*	+18°	0.00	10	*P*	2	+13°	+0.55	9	*O*
4*	+32	+0.02	5	*N*‡	3*	+18	+0.57	4	*P*
5*	+42	+0.03	11	*N*‡	4*	+32	+0.45	5	*N*‡
6*	+36	−0.23	3	*N*‡	5*	+42	+0.32	3	*N*‡
12*	+41	−0.10	3	*N*‡	6*	+36	+0.17	5	*N*‡
14	+57	+0.06	6	*N*	7	+20	+0.22	5	*O*
18*	+ 6	+0.03	10	*O*	8	− 2	+0.62	20	*O*
20*	−17	+0.03	14	*P*	10	+13	+0.59	4	*P*
28	+39	−0.02	15	*N*	12*	+41	+0.61	3	*N*‡
32	+72	+0.01	2	*N*	16	+33	+0.31	11	*P*
36	+39	−0.03	3	*N*	18*	+ 6	+0.68	6	*O*
45*	−32	−0.02	10	*N*‡	20*	−17	+0.28	16	*P*
49*	− 2	+0.02	7	*O*	24	0	+0.50	13	*O*
61*	+34	−0.03	18	*N*‡	40	0	+0.82	13	*O*
69*	−47	0.00	4	*N*‡	45*	−32	+0.28	5	*N*‡
89	−23	0.00	13	*N*	49*	− 2	+0.57	17	*O*
96	−25	+0.02	13	*N*	61*	+34	+0.37	3	*N*‡
100	+28	+0.07	17	*N*	65	−12	+0.59	3	*P*
112*	−25	−0.13	6	*N*‡	69*	−47	+0.35	5	*N*‡
					73	−11	+0.71	5	*P*
					85	+27	+0.46	4	*P*
					108	+28	+0.35	8	*P*
					112*	−25	+0.26	18	*N*‡
19		−0.01	170		23		+0.46	185	

* The field includes both normal and abnormal colors.

† *O* indicates a field within the zone of avoidance for extra-galactic nebulae, *P* one within the zone of partial obscuration and *N* a region of normal nebular density.

‡ A field of low nebular density occurs within a few degrees of the Selected Area.

mostly within the zone of avoidance (*O*) for nebulae or the bordering zones of partial obscuration (*P*). Eight of these groups, however, are in latitudes such that ordinarily only normal colors would be expected (*N*‡), but in each instance a sporadic field of low nebular density occurs somewhere in the immediate vicinity.

The mean latitude and the mean color-excess corresponding to the three degrees of obscuration, for the groups listed in the right-hand division of the table, are

	O	*P*	*N**
Latitude	6°	20°	36°
Color-Excess	0.57	0.48	0.35 mag.
No. Groups	7	8	8

The change in the color-excess with latitude is doubtless real, but its amount is not to be stressed because of the large fluctuations and the small numbers of groups.

All but one of the fields showing color-excess fall within an interval of about 150° in longitude, and none of them is very close to the direction of the center of the galactic system. The anti-center is, however, covered by the data, and for the fields in this general direction the color-excess is about the same as the mean for all the present data. This statement is not to be interpreted as an indication that color-excess does not depend on longitude, but merely as evidence that selective absorption is clearly operative in the direction of the anti-center as in other longitudes. A discussion of any dependence on longitude requires more extensive material than is now available for faint stars.[13]

The relation between color-index and spectral type used for the reduction of the observations requires comment. A compilation of Mount Wilson data on the international system gives for the interval A0 to K0 (ordinary giants) a range of 1.12 mag., a value in general agreement with other recent results[14] but considerably less than that found from early Mount Wilson measures.[15] The cause of this disagreement is not yet clear, but part of it is probably due to selective absorption, as many of the stars originally used are not far from the Milky Way. The important point, however, is that for A0 stars in unobscured regions the mean color-index on the international system (i.e., IPg − IPv) is not zero, but −0.14, with an uncertainty of 0.02 or 0.03 mag.

The explanation of this unexpected result, which is supported by strong evidence, is that the polar region is covered by a veil of obscuration, and when the zero point of the international photographic scale was fixed,[16] before there was any evidence of selective absorption, the choice was influenced by an unsuspected color-excess in the polar stars. The adopted zero point corresponds to zero color-index for the A0 stars of the Polar Sequence, but not for A0 stars in unobscured parts of the sky. A recent Mount Wilson investigation shows that for 271 stars north of 80° declination the relations are such that in this region the mean color index corresponding to A0 is −0.04. The *mean* color-excess for the polar cap 20° in diameter (*Draper Catalogue* stars, latitudes 18° to 38°) is therefore about

0.10 mag. The amount is small, but the abundance and consistency of the data upon which it is based are such that the result is accepted as significant. It is, moreover, in harmony with the fact that the nebular density in the polar region is below normal.

As a whole these results (limiting magnitude 13.5 photographic scale) strengthen the evidence that selective absorption is a wide-spread phenomenon and suggest a close correlation with the surface density of extragalactic nebulae. For any field in which the nebular density is low an excess of color apparently is to be expected for at least part of the stars in the field, presumably the more distant objects in general. Certain fields obscured by clouds so dense as to be practically opaque seem, however, to be exceptions to the rule. The fluctuations in the color-excess are large and apparently unrelated to the general appearance of the field. Finally, it is to be noted, as probably significant for the interpretation of results, that the value of the color-excess seldom if ever exceeds one magnitude and seems, therefore, to be subject to the restriction of an upper limit of about this amount.

[1] *Mt. Wilson Contr.*, No. 187; *Astrophys. Jour.*, **52**, 8–22 (1920).

[2] *Report Mount Wilson Observatory, Year Book Carnegie Institution*, **20**, 255 (1921). The values of the color excess originally published are here increased by 0.14 mag. to allow for a shift in the zero point of the relation between color index and spectral type. This change is explained in a later paragraph of the present communication.

[3] *Lick Observatory Bulletins*, **14**, 154–188, No. 420 (1930).

[4] *Mt. Wilson Comm.*, No. 111; *Proc. Nat. Acad. Sci.*, **19**, 222–228 (1933).

[5] *Publ. Washburn Observatory*, **15**, 217–259, No. 5 (1934).

[6] Cf. *Ibid.*, 245.

[7] Seares, Humason and Joyner, *Publ. Astron. Soc. Pacific*, **43**, 53–56 (1931); Seares and Joyner, *Ibid.*, 57–60.

[8] Cf. footnote 2.

[9] *Mt. Wilson Contr.*, No. 458; *Astrophys. Jour.*, **76**, 224–274 (1932).

[10] *Bergedorfer Spektral-Durchmusterung*, **1**, 1–218 (1935).

[11] *Lick Observatory Bulletins*, **13**, 68–91, No. 390 (1927).

[12] *Mt. Wilson Contr.*, No. 485; *Astrophys. Jour.*, **79**, 8–76 (1934).

[13] Cf. Stebbins and Huffer, op. cit., 247.

[14] Payne-Gaposchkin, *Harvard Annals*, **89**, 105–115, No. 6 (1935).

[15] Seares, *Mt. Wilson Contr.*, No. 226; *Astrophys. Jour.*, **55**, 165–237 (1922).

[16] Seares, *Mt. Wilson Contr.*, No. 97; *Astrophys. Jour.*, **41**, 206–236 (1915).

ON THE PHYSICAL CONDITION OF THE SUPERNOVAE

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There seems to be good evidence for the existence of a group of novae that are several magnitudes brighter absolutely than the galactic novae commonly observed. They have been called the supernovae. According to Baade and Zwicky,[1] who have assembled the evidence, they attain absolute visual magnitude -13 at maximum, with a small dispersion; this estimate is apparently based on a value of -14.7 for the absolute visual magnitude of the average galaxy. If the Harvard value[2] $-14.5_{pg} \equiv -15.4_{vis}$ is adopted for the absolute magnitude of an average galaxy, the absolute visual magnitude of an average supernova becomes -13.7. Thus the supernova S Andromedae, which, on the basis of $22^m.2$ for the distance modulus of the Andromeda nebula, had at maximum an absolute visual magnitude -14.7, was not far from typical in luminosity. Calculations based upon its relatively well observed light curve are probably reasonably representative, giving values for the radiated light and energy that are perhaps greater than the average by a factor of two.

At a time when the spectra of supernovae were unknown or enigmatic, it was reasonable, as suggested by Baade and Zwicky,[1] to assume that the conditions that produced them differed greatly from those that produce the spectra of the normal novae. At present, however, it has been shown that four of the supernovae differed spectroscopically from the normal novae essentially only in the radial velocities of the ejection of material. The spectra of S Andromedae[3] and Z Centauri[4] were recently shown to have consisted of wide bright lines and a continuous background; the latter star, at least, had a strong wide band at 4650, as well as indications of the presence of the Balmer lines.[5] A similar deduction had previously been made by Vorontsov-Velyaminov,[6] who classified the spectrum of Z Centauri as O. More recently the spectra of two supernovae obtained at Mount Wilson (in N. G. C. 4273 and N. G. C. 4303) have been published by Humason.[7] Both spectra, while "not easy to interpret," appear to have displayed the lines of hydrogen,[8] and their strongest feature seems, from the figure, to have been a bright band centered near 4650. The spectra are strikingly similar to the spectrum of Z Centauri.[9] From the widths of the bands in the Mount Wilson spectra Humason deduces a radial velocity of expansion of 6000 km./sec. The writer suggested a velocity of the order of 10,000 km./sec. for Z Centauri. The Mount Wilson value will be adopted for purposes of calculation.

It seems legitimate to conclude that the three spectra, of Z Centauri,

and of the supernovae in N. G. C. 4273 and in N. G. C. 4303, all contained wide bright lines of hydrogen of moderate strength, and a stronger wide bright band centered near 4650, which probably consisted chiefly of the group of N III lines that are a conspicuous feature of galactic novae at a relatively early stage. In the notation of the Commission on spectral classification of the International Astronomical Union,[10] all three spectra could be described as *Qun!;* they differ from those of galactic novae only in the extreme width of their bright bands. The spectrum of S Andromedae was examined only visually, so that the blue region at 4650 was not well placed for observation. A discussion of the published descriptions leads to the conclusion[3] that the spectrum contained wide bright lines, and we shall assume that S Andromedae was spectroscopically a typical supernova, as it appears to have been typical in light curve[11] and fairly typical in luminosity.

For an ordinary nova, a spectrum of Class *Qu* is associated with a temperature not greater than 30,000°; if the nebular lines N_1 and N_2 of O III are present, they are at least inconspicuous. The temperature of a nova in the nebular stage (*Qy*, *Qz*) is[12] about 50,000°, which must therefore be regarded as an *upper* limit for these three supernovae at the dates on which their spectra were secured, because they had not yet reached Class *Qy* or *Qz*. The available evidence concerning the spectra of novae indicates that the maximal temperatures were probably even lower.[13] It therefore seems that the exceedingly high surface temperatures contemplated by Baade and Zwicky* for the supernovae must be ruled out by observation, and that these extremely bright stars should now be regarded as differing from other novae only in their luminosities and in the velocities of expansion. A few rough calculations will show that in other respects a supernova resembles an ordinary galactic nova.

In what follows we adopt a velocity of expansion 6×10^3 km./sec., a total range of 14 magnitudes (near the minimum value for S Andromedae), a time of rise, t, of two days (of the order accepted by Baade and Zwicky), and a ratio, $\gamma = 10$, of maximal to minimal surface brightness, corresponding to a ratio of about 3 in absolute temperature, probably a maximum value. Then according to the simple relation given by Gaposchkin[14]

$$R_0 = \frac{1}{8}\frac{vt\gamma^{1/2}}{u^{1/2}}$$

where v is the velocity of expansion, u the total range in brightness and R_0 the radius before the outburst. Inserting numerical values we obtain $R_0 = 8R\odot$, a radius appropriate to a giant star like Capella, with an absolute visual magnitude about zero. If we suppose, therefore, that a supernova has an absolute visual magnitude zero before its outburst, we obtain, with a range of fourteen magnitudes, an absolute visual magnitude at maximum

of -14.0, in good agreement with the observed value -13.7, and an independent check on the conditions adopted.

On the basis of the same simple theory we obtain for the maximal radius a value of 1500 times the solar mass—an increase of radius by about 200 times. The proportional increase of radius for normal novae is of the same order.[15] The similarity, of course, results from the fact that the visual ranges of the two types of nova are not very different.

For a radius of 1500 $\odot$ and an absolute visual magnitude -14.7, we should obtain, on the somewhat unlikely assumption of black-body radiation, a temperature of 22,000° by the method used by Baade and Zwicky, a result that confirms our conclusion that the temperature is not excessively high. A value of 22,000° is indeed not unreasonable in view of the ionization temperature of 30,000° deduced shortly after maximum, and of our knowledge of the post-maximum increase of effective and ionization temperatures for other novae.

The large differences between our temperatures and those of Baade and Zwicky (which are of the order of 10^6 degrees) are entirely a consequence of the different adopted maximal radii. In the light of present spectroscopic knowledge there seems little justification for supposing, as they do, that the maximal radii of supernovae are actually *smaller* than those of normal novae. On our view they are *larger* in rough proportion to the radial velocities. From a simple geometrical standpoint, at least, this picture seems acceptable, since with such high velocities, far exceeding the velocity of escape, gravitation can play no part in the motions and ultimate equilibrium of the ejected material; the dimensions finally attained should be governed only by the amount of matter, the speed with which it is ejected, and the energy incident on it from below (for discussion on this point I am indebted to Dr. Fred L. Whipple).

Baade and Zwicky concluded that the mass of the energy sent out by a supernova in the form of radiation may be of the same order as the original mass of the star. But this conclusion is very sensitive to the adopted surface temperature. If the calculations are repeated for maximal temperatures of 13,000°, 20,000°, and 32,000°, we obtain, for the total energy radiated per second by S Andromedae at maximum, 5×10^{41}, 3×10^{42} and 2×10^{43} ergs, respectively. On integrating the light curve, the *total* amounts of energy radiated at these three temperatures (assumed constant) are seen to be 4×10^{46}, 2.5×10^{47} and 1.6×10^{48} ergs, respectively, during the first two months of the star's brightening.** When these quantities of energy are converted into grams, we have, for the total loss of mass by radiation at the three temperatures considered, 5×10^{25}, 3×10^{26} and 2×10^{27} grams, respectively. None of these quantities is significant in comparison with the mass of an ordinary star, such as we suppose the supernova to have been before its outburst. And since the average supernova seems to radiate

about half as much light as S Andromedae, the above masses should probably be halved if they are to represent the general case.

It should be noted that the above calculations were based on the assumption, used by Baade and Zwicky, that the nova radiated like a black body. More recent researches on the spectral energy distribution for stars with expanding atmospheres[16] have shown that this assumption can be replaced by a more precise one. But it is unlikely that even when allowance is made for an excess of energy in the ultra-violet portion of the spectrum, the mass of the radiated energy will approach that of the star itself.

The spectra do not lend themselves to quantitative work. One qualitative conclusion can, however, be drawn from them. Their bright bands are about as strong as in the spectra of normal novae at a similar stage; thus it is probable that about the same proportion of the surface is involved in the outburst. The loss of mass, by radiation and ejection, is therefore probably in about the same ratio to the total mass for both sorts of novae.

It seems possible that the supernovae are merely novae that have developed from giant rather than from dwarf stars (it is suggestive in this regard that their dispersion in absolute magnitude at maximum is noted by Baade and Zwicky as small, while it must be larger for "ordinary" novae, if van Maanen's estimate[17] of an absolute magnitude not brighter than zero for Nova Sagittae No. 2 is correct). If so, their frequency (perhaps a millionth of that of normal novae) may well represent the relative commonness of the giant and dwarf stars from which the two types originate.

Summary.—It has recently been shown that the spectra of supernovae display features similar to those of normal galactic novae, but with bright lines that are considerably wider. If it is accordingly assumed that their surface temperatures, a week or two after maximum, are normal for novae, and of the order of 20,000°, we are led to maximal dimensions that are larger than those of galactic novae in rough proportion to the radial velocities (deduced from the widths of the bright lines). The outburst of a supernova thus seems to be a phenomenon that differs only in scale from that of a normal galactic nova. The total energy radiated during an outburst is of the order of 10^{48} ergs, or 10^{27} grams, and if we suppose the star to have had a normal stellar mass before brightening, the loss of mass by radiation is therefore negligible.

* It is an interesting speculation to inquire what kind of spectrum would be given at the temperature of 10^6 degrees mentioned by Baade and Zwicky. The radiation would consist principally of soft x-rays. All the lighter atoms, common in the atmospheres of ordinary stars, would probably be stripped (the corresponding level of ionization is about three thousand volts), and a qualitative guess suggests that the spectrum would show no lines strong enough to be observed in contrast with the continuous spectrum, since the only surviving atoms (those of high atomic number) are cosmically rare.

** Baade and Zwicky considered that the main radiation of energy took place within 25 days of maximum.

[1] Baade and Zwicky, these PROCEEDINGS, **20,** 254 (1934).
[2] Shapley, *Ibid.*, **19,** 594 (1933) (H. Rept. 92).
[3] C. Payne Gaposchkin, *Ap. Jour.*, **83,** 245 (1936).
[4] C. Payne Gaposchkin, *Ibid.*, **83,** 173 (1936).
[5] Johnson, *H. B.* 902 (1936).
[6] Vorontsov-Velyaminov, *Russ. Astr. Journ.*, **8,** 42, 27 (1931); *Astr. Nach.*, **242,** 208 (1931); "New Stars and Galactic Nebulae," 221, 261 (1935).
[7] Humason, *P. A. S. P.*, **48,** 110 (1936).
[8] Humason, loc. cit., p. 112.
[9] *Harv. Ann.*, **76** (37, and Plate 2) (1913); Johnson, loc. cit.
[10] *Trans. Int. Astr. Union*, **1,** 98 (1922).
[11] Lundmark, *Kungl. Vetens. Svensk. Hand.*, **60,** No. 8, 55 (1917).
[12] Vorontsov-Velyaminov, *Zeit. Ap.*, **10,** 365 (1935).
[13] Menzel and Payne, these PROCEEDINGS, **19** (No. 7) (1933); see also F. L. Whipple and C. Payne Gaposchkin, *Harv. Circ.* 412 (1936), for the increase in temperature of Nova Herculis immediately after maximum.
[14] S. Gaposchkin, *Harv. Bul.* 899 (1935).
[15] S. Gaposchkin, *Harv. Bul.* 901 (1935).
[16] Kosirev, *Mon. Not.*, **94,** 430 (1934); F. L. Whipple and C. Payne Gaposchkin, *Harv. Circ.* 413 (1936).
[17] Van Maanen, *P. A. S. P.*, **46,** 282 (1934).

A MODEL IMITATING THE ORIGIN OF SPIRAL WALL STRUCTURE IN CERTAIN PLANT CELLS

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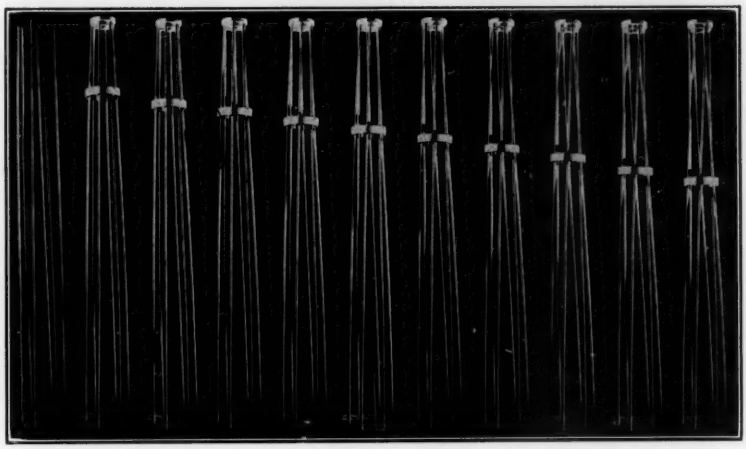
The walls of many plant cells show spiral structure. When a living cell with spiral structure elongates, spiral growth results, accompanied by rotation or twisting of the cell about its principal axis. Spiral growth of this type is particularly evident in the mature sporangiophore of Phycomyces (Oort, '31). No satisfactory explanation has been given for the origin of spiral structure, and hence of spiral growth, in the primary wall of a tubular cell of this type.

Since the steepness of the spiral in the cell of Phycomyces can be experimentally modified during growth (Castle, '36), it appears that spiral structure in the primary, growing wall is not rigidly predetermined, but that it must be due to some kind of equilibrium condition of forces existing at the growing region. Furthermore, it is probable that these forces are exerted on and in the cell wall itself, and that they result from the interaction between outward turgor pressure and elastic forces within the wall. On the assumption that these elastic forces might be concerned in the

origin of spiral structure, the mechanical model shown in Plate 1 was devised.

The model consists of six wooden dowels, three feet in length, set rigidly in a wooden base (Fig. 1). The dowels are free at the top, but a wooden ring pushed down around them causes them to thrust inward against a spool at the top. A rim on the spool rests on the ends of the dowels and keeps it from sliding down between them. The spool has a smaller diameter than the circle into which the dowels are set in the base, so that the whole



1 2 3 4 5 6 7 8 9 10 11

PLATE 1

The mechanical model illustrating a method of origin of spiral structure. Description in the text.

Figure 1. The six dowels fixed in a wooden base tend to stand nearly vertically.

Figure 2. The compressing ring has been pushed over the dowels, causing them to thrust slightly in against the spool.

Figures 3 to 11. Spiral twisting of the rods as the ring is pushed down. Development of the twisted configuration is most clearly seen with the page horizontal and the eye on a level with and close to the bottom of the page. Note that in passing from figure 2 to figure 11 the spool has been rotated about one-sixth of a revolution.

structure tapers from bottom to top. In figure 2 the dowels have been bent in until they just touch the spool. In successive pictures the ring is pushed farther down, increasing the bending stress on the dowels. As may be seen, the dowels resolve the forces acting on them by all inclining to one side (or to the other[1]), giving a spiral structure. We may suppose that under these conditions the stored elastic energy of the system is at a minimum.

It is interesting to consider how far the model imitates conditions which might be present at the growing region of a cell of the Phycomyces type.

(1) *Configuration.*—Spiraling in the model seems to depend on bending stresses which force the surface of the structure into a complex curve which, seen in lateral profile view as in figure 11, is no longer simply concave toward the center of the model as in figure 2. In the complex curve an inflection point occurs. The same is true of the growth zone of the mature sporangiophore of Phycomyces (Fig. 12), which is distinctly tapered in this region and which exhibits in profile a similar complex curve.

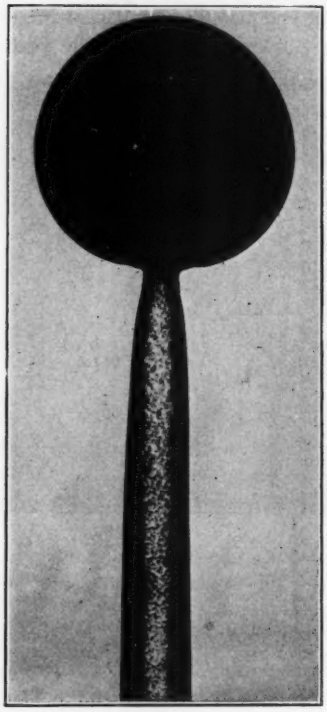


FIGURE 12

Sporangiophore of Phycomyces with spherical spore mass on top. The growth zone begins close below the sporangium and extends downward 1 to 2 mm. Note the curvature of its surface. × 93.

(2) *The Spool.*—The upper end of the growth zone coincides with the base of the columella where the tubular sporangiophore joins the sporangium. At this point in the cell a thickened chitinous ring occurs which is in a position to resist inward pressure as does the spool in the model.

(3) *The Compressing Ring.*—Nothing directly resembling this ring exists in the cell, where stresses on the cell wall must result from turgor pressure from within, osmotically generated. In general, pressure from within will tend to straighten out a structure which has been previously twisted. But no straightening occurs in the cell, which continues to grow by means of internal pressure while maintaining its spiral structure. Why pressure does not "unwind" the spiral in this case is not clear, unless graded differences in lateral, cohesive forces between elements in the stretched cell wall at different levels along the growth zone produce a system of stresses which resemble those in the model, and which result in a continuous tendency to twist. The similar configurations of cell and model appear to support this idea, although the mechanism by which bending stresses are obtained in elements of the cell wall is obscure.

(4) *The Dowels.*—A primary assumption in the comparison of cell and model is that some type of elastic element is present in the cell wall. So

much has been made in recent years of an increased plasticity as accompanying elongation of plant cells that it is useful to recall some of the earlier work on the elasticity of growing cells. Laurent (1885) showed that the osmotic pressure of the Phycomyces cell may reach 8 atmospheres, and that the growth zone is elastically stretched by some 6 per cent of its length. When the turgid cell is plasmolyzed, for example, he found that the growth zone alone contracts measurably, and to the extent indicated. Moreover, within this zone a greater rate of growth is correlated with greater elastic contraction on plasmolysis. Clearly the growth zone of this cell is the seat of considerable elastic force.

In the model the elastic members have the form of continuous rods. The analogy with the secondary wall structure of plant cells is satisfactory, since cellulose or chitin chains of considerable length and thickness are generally agreed to form the structural framework of the wall. It is reasonable to attribute rigidity and elasticity to this framework.

With regard to the orientation of these rods a question arises. In the model they are initially parallel to the long axis of the "cell." We should expect such an arrangement, if reduced to the molecular level, to be optically anisotropic in surface view with its greatest (n_γ) axis[2] parallel to the "cell" axis. This arrangement shows in surface view so-called positive birefringence, and typically occurs in the walls of adult elongated cells. It has been called by Frey-Wyssling ('35) "fibre structure." The primary, growing walls of plant cells, however, have been described as either apparently isotropic or weakly anisotropic in surface view, with the n_γ axis perpendicular to the cell's long axis (Bonner, '35). This condition exhibits in surface view so-called negative birefringence, and has been called by Frey-Wyssling ('35) "tubular structure." Oort and Roelofsen ('32), for instance, found that the growth zone of Phycomyces after bleaching and staining was optically a typical tubular structure. The writer has also found negative birefringence in surface view at the growth zone of Phycomyces without previous chemical treatment.

There is, however, disagreement between the results of optical and other methods of study of the primary wall. According to Oort and Roelofsen ('32) the micellar orientation judged by birefringence is across and around the cell axis (tubular structure). But if the internal pressure in the cell is artificially raised by squeezing, they found that the growth zone split open in a steep spiral practically parallel to the cell axis. They concluded that the split occurred parallel to the n_β axis of the chitin micelle. It is hard to credit this conclusion, since cellulose structures are ordinarily most easily split parallel to the n_γ axis, where the chains are supposed to be bound together side to side by secondary valence forces. A break parallel to the n_β axis is resisted by very large forces, as shown by the high tensile strength of fibres.

For the model which has been described, it is interesting that while its linear arrangement of elastic members appears to be contrary to evidence of cell structure from polarization optics, this evidence itself is called into question by evidence from bursting experiments. In view of our ignorance of the significant structure of any primary wall, use of the model in its present form may help to interpret the orienting effect of mechanical forces on the growing cell wall. There is, however, no reason to suppose that all types of spiral structure in plant cells have a single mode of origin.

Summary.—A mechanical model is described in which bending stresses on a system of elastic rods produce a spirally twisted configuration. The possible rôle of similar elastic forces in determining spiral structure and spiral growth of the primary wall of the spore-bearing cell of Phycomyces is discussed.

[1] With an ideally symmetrical structure, equal numbers of right-hand and left-hand spiral configurations would be expected to result from a large number of successive trials. The model shown in Plate 1 usually showed left-hand spirals, due to initial asymmetries in the dowels. A left-hand spiral is here defined as spiraling in the direction of the thread on a left-hand screw. It is interesting to note that Oort ('31) found with Phycomyces that left-hand spirals were the rule in a population of cells.

[2] The axes here referred to are those which characterize the so-called index ellipsoid of anisotropic bodies. The axes are given by the values of refractive index in the three planes of space, and by convention $n_\gamma > n_\beta > n_\alpha$. For cellulose n_γ coincides with the long axis of the micelle. It is useful to recall that as far as is known n_γ, and therefore the chief axis of the cellulose micelle, is always parallel to the cell surface in plant structures (Frey-Wyssling, '35).

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A NEW RED ALGA FROM NEW ZEALAND

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Communicated April 29, 1936

Mr. R. M. Laing recently transmitted to Dr. W. A. Setchell some specimens of Zostera from Lyttleton, in the South Island of New Zealand, for study and determination. The latter, while soaking out and examining the specimens, noticed a small red alga growing on the margins of the outer ends of the leaves and submitted the same to me for study. The specimens seem to me definitely to belong to an undescribed species with affinities most closely with *Erythrotrichia polymorpha* Howe (1914, p. 77).

There are very few previous references to the genus as occurring in the waters of New Zealand. The first reference, so far as the writer is at present able to ascertain, was that of J. D. Hooker (1855, p. 264), who reported the presence of *Bangia ciliaris* Carmichael in Cook's Straits, the type locality of which is Appin, Scotland. Harvey, *in* Hooker (1867, p. 716), reports the same species from Cook's Straits, with a more detailed description than the original given by Carmichael. Harvey does not indicate that he examined any material either fresh or preserved, but states that it was "parasitic on *Zostera*, Cook's Straits, Lyall," the same statement as was made by Hooker concerning its habitat and locality. Harvey also refers to his Phyc. Brit., t. 322, which reference concerns material from Cherbourg which he claims to be equivalent to Captain Carmichael's *B. ciliaris* as well as to the *Porphyra Boryana* Mont., but allied it with Areschoug's genus *Erythrotrichia*. From this time until 1900 there had been a variety of interpretations of Carmichael's species although apparently no one had made a critical study of the type which is preserved in the Hookerian Herbarium at Kew. In this year Batters (1900, p. 374) published the results of a careful examination of the type material, and this, in connection with the study of the description and figures of Harvey (Phyc. Brit., pl. 322) of *Bangia ciliaris* Carm. from Scotland, led him to conclude that the plants from Cherbourg referred by Thuret to *B. ciliaris* were not to be allied with Carmichael's species but that Berthold's *E. discigera* or *E. obscura* represents Carmichael's *B. ciliaris*, thus leaving unsettled the identity of Thuret's plant from Cherbourg. Laing more recently (1928, p. 55) reports a plant under the name *Erythrotrichia ciliaris* (?) (Carm.) Batters which he collected at Akaroa Harbor, New Zealand, June 2, 1904, and which he submitted to Major Reinbold, who identified it as *Bangia ciliaris*. Laing's later examination of the material revealed that the erect filaments arise from a basal disc, and he expresses some doubt

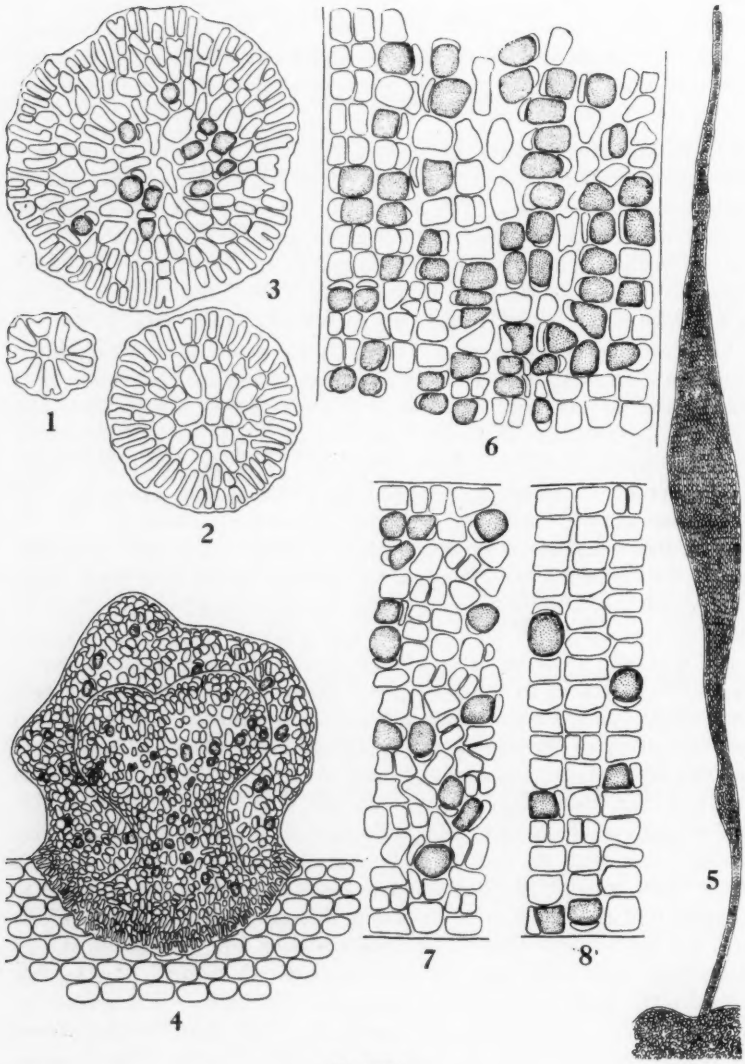

PLATE 1

(Description on opposite page.)

as to the identity of the species as being the same as any of the European species of the genus.

From these studies it seems to the writer that the plant from New Zealand should not be united with any of the described European species of the genus, and that it is more closely related to the South American species, *E. polymorpha*, which Howe (loc. cit.) has so amply described and figured. Howe dwells at considerable length upon the forms which the basal disc may assume in his species, according to the host upon which it grows. The New Zealand plant differs from Howe's species in having smaller discs on the surfaces of the host, and thicker tuberculate discs along the margins, in having longer and wider erect filaments with monosiphonous base and apex, and in the smaller marginals cells of the disc.

The material from New Zealand has thus far been found only on the leaves of *Zosterea*, but on this host it assumes different forms according to the position in which it gets started. On all of the examples which the writer has examined, the plants are most abundant along the margins of the leaves, and the youngest found were along the margins rather than on the surfaces. However, relatively young discs were abundant among mature fruiting discs in this latter position.

A peculiar condition of apparent dimorphism as regards the occurrence and position of erect filaments seems to exist in the New Zealand plants, similar to that reported by Howe in the South American species. He found that on certain hosts the erect filaments arise from discs but were absent from fruiting discs on other hosts. In the New Zealand species, the erect filaments all arise from the marginal plants, none from the discs on the flat surfaces of the leaves; but not all of the marginal plants produce erect filaments. The mature plants, so far as the discs are concerned, are very different in form on the same leaf, those on the flat surface never becoming more than one layer of cells thick, although the cells in the center of the disc are larger and usually much more elongated perpendicularly than those around the periphery, while the plants along the margins of the

DESCRIPTION OF PLATE 1

Erythrocladia Hunteriae

Figures 1, 2 and 3. Showing three stages in the development of the monostromatic discs on the surface of the leaves of the host. ×500.

Figure 4. Showing a fruiting, tubercular disc attached on the margin of the leaf without erect fronds. × 250.

Figure 5. Showing a relatively immature erect frond from a tubercular base. Sedi-diagrammatic.

Figure 6. Showing a surface view of a portion of a medium-sized frond producing an abundance of gonidia. × 600.

Figures 7 and 8. Showing a surface view of a portion of the frond, 7, with irregular arrangement of the cells, and 8 with cells arranged regularly in rows crosswise and lengthwise. × 600.

leaf become tubercular in form and more than one layer of cells thick in that which is virtually the center of the disc. Discs in both positions produce gonidia. Laing's observations on the material from Akaroa Harbor apparently did not reveal this polymorphic condition; at least no such results were mentioned.

The polymorphic condition manifest in this species brings up the question of the validity of Schmitz's genus *Erythropeltis*. There need be no doubt that all of the specimens of the species here proposed belong to one entity. The gonidia in the discoid and tuberculate forms and in the erect filaments are all similar; the discs on the surface merge directly into those on the margins; and while there are no erect filaments from the surface discs, not all of those on the margin give rise to them.

The discs on the surface of the leaves have all of their characteristics answering perfectly to the description of *Erythropeltis* as outlined by Schmitz. This may be a mere coincidence, but the question is open to much doubt as to whether the genus *Erythropeltis* is entitled to be accorded separate generic rank.

The species may be described, diagnosed and figured as follows:

Erythrotrichia Hunteriae sp. nov.

Plate—figures 1–8

Frond composed of a monostromatic disc only, or of a tubercular cushion giving rise to numerous erect, more or less ligulate filaments 7–10 mm. high; the basal portion assuming two forms according to the position of origin on the host, viz., a circular disc, 100–150 μ diam., composed of a single layer of cells but much thicker in the central portion and not giving rise to erect filaments, growing on the flat surface of the leaf of the host, *Zostera;* and tuberculate, more or less confluent forms up to 190 μ diam. and 2 or more cells thick, mostly thicker than the horizontal diameter, growing along the margins of the leaf, and giving rise to the erect filaments; growth of the disc marginal, width being attained by marginal cells becoming cuneate, finally furcate, and subsequent horizontal or oblique division of marginal cells 3–5 $\times$ 8–15 μ; fruiting asexual, by gonidial formation, characteristic of the genus, in both the basal and erect filamentous parts, occurring in the former first; cells of the basal, discoid and tubercular parts quite variable in shape and size according to the position they occupy; erect filaments up to 10 mm. long, monosiphonous for considerable distance at the base and apex, varying in width in the same filament, monostromatic and up to 16 cells wide; cells mostly quadrate, 8–11 μ diam., arranged for the most part in rows both lengthwise and crosswise but occasionally very irregular; gonidia formed in the usual way for the members of this genus, 11–15 μ diam.

Frons biformis, nunc, in superficiebus planis foliorum plantarum hostis crescens, disciformis unistratosaque, nunc, in marginibus foliorum hostis crescens, discoideo-pulvinata et filamenta curta erectaque emittens; discis 100–190 μ diam.; filamentis erectis plus minusve ligulatis, 7–10 mm. altis, basi apiceque monosiphoneis, usque ad 16 cellulis in latitudine et 1-cellula in portione central in crassitudine compositis; gonidiis 11–15 μ diam., e discis basalibus et filamentis erectis productis.

The Latin diagnosis was furnished through the kindness of Dr. W. A. Setchell.

Growing on the leaves of *Zostera novazelandica* Setchell. Lyttleton, Cook's Bay, New Zealand. Collected by Miss Hazel Hunter, June 23, 1935, and contributed by Mr. R. M. Laing. Type, Herbarium University California No. 510681.

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THE SYSTEM ALBITE–FAYALITE

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Introduction.—This paper is a record of a study of phase equilibrium at high temperatures in mixtures of two silicate compounds, $NaAlSi_3O_8$ and Fe_2SiO_4, which are known among natural minerals as albite and fayalite, respectively.

These minerals are found together in rocks of wide-spread occurrence and it is expected that a knowledge of their equilibrium relations may throw light upon the genesis of such rocks. The investigation is a first step in the examination of mixtures of alkali alumino-silicates and ferrous silicates.

Methods.—The thermal study is carried out in a platinum-wound re-

sistance furnace, the crucible with its charge being suspended in the furnace. The temperature of the appearance or disappearance of a phase is determined by the method of quenching which consists in holding the charge at a constant measured temperature for a period of time sufficient to obtain equilibrium, then quenching it by dropping it into mercury and examining the product under the petrographic microscope to determine the phases present. During the instantaneous cooling thus effected no new phases are ordinarily formed and microscopic examination reveals the phases present at the furnace temperature. By heating any given mixture at a number of temperatures the phase changes and the temperatures at which they occur are determined. The method of quenching has proved a most effective mode of attack upon the problem of phase equilibrium in silicates in general.

The distinctive feature of the method as applied to ferrous silicate compositions is that a stream of nitrogen is passed through the furnace to provide a neutral atmosphere and the charge is contained in a crucible of pure electrolytic iron, contact with metallic iron ensuring that most of the iron of the charge is in the ferrous state. Iron-bearing silicate melts in equilibrium with metallic iron always contain a small portion of their iron in the ferric state, a matter which is discussed fully in an earlier paper.[1] The actual amounts in the present melts are given in table 1.

TABLE 1

CHEMICAL AND THERMAL RESULTS UPON MIXTURES OF ALBITE AND FAYALITE

IRON OXIDES BY ANALYSIS		COMPOSITION IN TERMS OF		THEORETICAL IRON CONTENT	TEMPERATURE OF COMPLETE MELTING ± 3°	PRIMARY PHASE
FeO	Fe_2O_3	ALBITE	FAYALITE	FeO		
...	...	100	...	...	1122	albite
4.90	0.62	92.5	7.5*	5.3	1088	albite
10.03	0.63	85.0	15.0*	10.6	1055	albite
16.49	0.60	76.0	24.0*	16.9	1079	fayalite
22.91	0.47	67.0	33.0	23.3	1098	fayalite
28.30	0.87	58.5	41.5	29.2	1109	fayalite
35.31	0.94	48.5	51.5	36.3	1122	fayalite
43.76	1.39	36.0	64.0	45.1	1133	fayalite
50.60	1.25	26.5	73.5	51.8	1147	fayalite
56.19	1.40	18.5	81.5	57.4	1160	fayalite
62.05	1.54	9.5	90.5	63.8	1182	fayalite
68.36	2.25	...	100.0	70.5	1205	fayalite

* Temperature of beginning of melting of completely crystallized mixture 1050° ± 5°.

Composition Relations.—Mixtures of albite and fayalite lie upon a join in a more general system, nepheline ($NaAlSiO_4$)–FeO–SiO_2, now under investigation. In the triangular diagram representing a system with these compounds as the chosen components (Fig. 1) albite and fayalite become binary compounds and all mixtures of the compounds lie upon the straight line joining them. Some of the difficulties attendant upon the investigation

of iron-bearing silicates are well illustrated by our attempts to prepare mixtures lying along this line. The procedure and the theoretical considerations involved in the procedure will therefore be discussed briefly with special reference to one particular mixture. In order to obtain a mixture having the approximate composition 40 per cent albite 60 per cent fayalite (x, Fig. 1) we mixed sodium disilicate, silica and Fe_2O_3 (as a source of FeO) in the calculated proportions and melted them together 3 times with intermediate grinding in a platinum crucible in air and then 3 times,

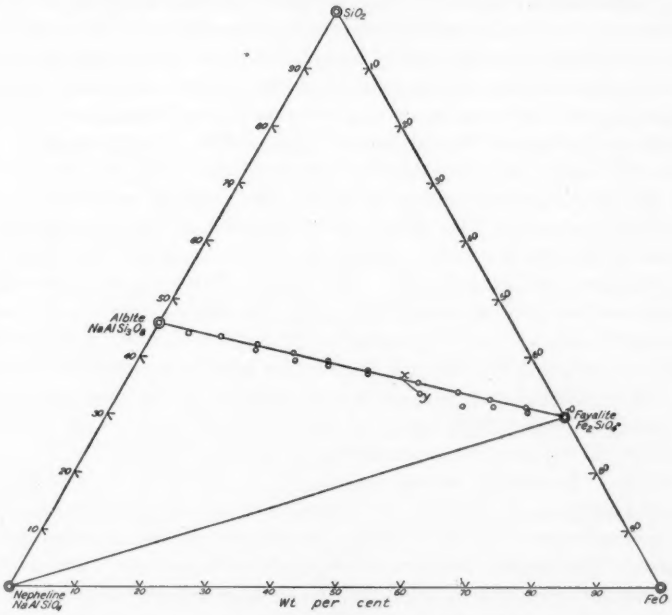

FIGURE 1

Diagram of the system nepheline ($NaAlSiO_4$)–FeO–SiO_2, showing investigated mixtures on the albite-fayalite join.

again in a platinum crucible, in a gas furnace. Under these conditions some of the iron of the charge is taken up by the platinum crucible and some of the iron oxide remaining in the charge persists in the ferric state. We then melted the product in an iron crucible in an atmosphere of nitrogen. Under these conditions most of the ferric oxide reacts with the iron of the crucible to give ferrous oxide and there is thus an addition of iron to the charge which is compensatory to the previous loss of iron to the platinum crucible. The state of balance between these two effects cannot be predicted. The amount of iron in the final product is determined only by

analysis. In the present mixtures the net effect is always an enrichment of the end-product in iron. The particular mixture under discussion was found to contain a great excess of FeO. The content of FeO aimed at in the mixture is 42.2 per cent. Upon analysis the charge after the above procedure was found to contain 46.2 per cent total iron oxides expressed as FeO (y, Fig. 1). For the purpose of solving relations in the general system represented by figure 1 this aberrancy of the composition of the product makes no difference because the relative proportions of all the other ingredients remain the same whatever vicissitudes the iron content experiences, and the composition of the final product must lie upon a line passing through the composition calculated from the initial ingredients and the FeO apex of the general triangle (see Fig. 1). In order to plot the final composition it is only necessary to determine the iron content and to place a point on that line at the determined value of FeO. For the mixture now under discussion the point lies at 46.2 per cent FeO (y, Fig. 1). By covering the area of the general triangle with mixtures so made, a variety of compositions is obtained from which are determined all the equilibrium relations of the whole system. Values for points along any join may then be obtained by interpolation. We wished, however, to have direct determinations upon mixtures lying upon the albite-fayalite join, and to accomplish this we made mixtures in the manner described, determined their iron content, thus placing them in the general composition triangle, and then modified their composition by addition of the amount of silica necessary to bring them upon the albite-fayalite join. This condition was checked by another determination of the iron content.

Results.—The results are expressed in figure 2 and table 1. The diagram is of the simple eutectic type. The liquidus of fayalite is of unusual shape but reversed curves of like character have been observed in other silicate systems. The eutectic mixture is rich in albite (84 per cent), and the temperature of the eutectic is 1050° ± 5°C. The liquidus of albite is, within the error of measurement, a straight line. From most silicate mixtures albite crystallizes with great reluctance, if at all, on account of the great viscosity of the liquids, but fayalite effects such marked reduction of the viscosity that from mixtures in the albite field there are formed overnight good crystals of albite, tabular //010, upward of 0.2 mm. across and showing the characteristic twinning displayed by the natural mineral.

General Considerations.—The fluxing action of fayalite was, of course, an expected effect and by adding fayalite or other iron-bearing silicates to the very viscous alkali alumino-silicate mixtures, of which the albite composition is a type, we expect to be able to solve many of the equilibrium relations in these recalcitrant silicate mixtures. We have used fayalite in our first attempts in this direction partly on account of its simple character but also because fayalite-bearing rocks rich in these alkali alumino-

silicates (feldspars and feldspathoids) are found in many parts of the earth and we wish to throw light upon their genetic relations. One of us (B.) has collected such rocks in the Great Rift Valley of Africa where they are represented among the rhyolites, trachytes and phonolites.[2] They are found in the volcanic girdle of the Japan Sea,[3] in islands of the Mediterranean,[4] of the South Atlantic[5] and again of the North Atlantic[6] and are evidently connected with a certain type of orogeny though upon the nature of this connection we have nothing better than surmise. The physico-chemical picture in the case of such rocks is, however, a fairly definite one. It is established by a great number of equilibrium studies of silicate melts and confirmed by the relations in rocks themselves that among the feldspathic constituents of rocks the alkali feldspars are the low-melting types and that their relations are such as to bring about their concentration in the residual liquids from fractional crystallization. It is also established

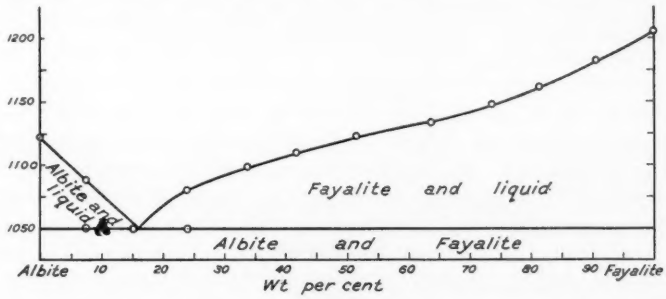

FIGURE 2

Equilibrium diagram of the system albite–fayalite. Circles indicate determined points.

in the same manner that among the ferromagnesian constituents of rocks the iron-rich members have the same relation to the magnesia-rich and lime-magnesia-rich members. In their high content of alkali feldspars and in the presence of the iron-rich silicate, fayalite, the fayalite rhyolites, trachytes and phonolites thus have the ear-marks of residual liquids from the fractional-crystallization of more complex and more "basic" magmas. There are, however, those who hesitate to accept this as the actual mode of origin of such rocks. It is suggested that the iron silicates would suffer even more marked concentration in residual liquids than would the alkali feldspars, whereas in point of fact the rocks in question contain alkali feldspars in great preponderance. The results upon the system albite–fayalite, certain mixtures of which may be regarded as representing somewhat simplified fayalite trachytes, give direct evidence on this question for the silicate pair concerned. The low-melting liquid in this case has

84 per cent albite and we know enough of relations in our general system (Fig. 1) to be able to say that the conditions are similar in mixtures with an excess of silica (simplified fayalite-rhyolites) and also in those with a deficiency of silica (simplified fayalite-phonolites). While we have made only a first step in the investigation of these extreme liquids it is plain from the results of this study that the moderate content of iron silicates in rocks rich in alkali feldspars cannot be urged as a feature militating against the acceptance of the rocks as substantially representative of the residual liquids from the fractional-crystallion of more complex "basic" magmas.

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FREQUENCY OF "CELL-LETHALS" AMONG LETHALS OBTAINED AT RANDOM IN THE X-CHROMOSOME OF DROSOPHILA MELANOGASTER

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The work to be reported in this paper is a by-product of experiments conducted in 1933 and 1934 when an attempt was made to determine the phenotype of a deficiency homozygous for certain known loci.[1] Deficiencies involving 12 short regions and including known loci of the *X*-chromosome were tested and in all but one case they were found to be cell-lethal. In the course of this experiment a number of *X*-chromosome lethals which occurred at unselected loci were also tested for the cell-lethal effect. The results of these tests will be described here.

Methods.—All lethals under consideration here were induced by x-ray treatment. All of them are *X*-chromsome lethals. They were picked up at random in the second generation from matings *m Mn f/m f* ♀ × x-rayed *y v* ♂.[2] The presence of *y*, *v*, *m* and *f* factors made it possible to test for crossing-over irregularities throughout almost the entire length of the chromosome and thus to determine whether or not a chromosomal abnormality was present. Only those lethals were used here which were free from

chromosomal abnormalities, since it has been found that frequently cell-lethal tests cannot be made if such an abnormality is present.

It has been shown by Bridges[3] that on females heterozygous for *Mn* there frequently appear small patches of wild-type tissue. He interpreted this as being due to the elimination of the *Mn* chromosome in the course of somatic cell divisions. After investigating this problem with somatic minutes, Stern[4] reinterpreted Bridges' results. He presented evidence for the occurrence of somatic segregation of *X*-chromosomes by which twin patches are formed, one patch representing the cell lineage of a cell carrying one *X*-chromosome and the other, the cell lineage of the cell carrying the other *X*-chromosome. Since *Mn* is a cell-lethal, the patch having the *Mn* chromosome only is not formed, and consequently only the patch representing the other homologous chromosome appears. If, therefore, the other chromosome carries a lethal to be tested and that lethal is a cell-lethal, no patches are expected to appear on *Mn/l* flies; if on the other hand the lethal is not a cell-lethal, single patches are expected to show. Stern[4] has shown that during such somatic segregation crossing-over occurs and hence a small number of single patches are produced representing the cell lineage of a chromosome from which the lethal factor has been removed through crossing-over. The test for a cell-lethal effect by this method, therefore, consists in determining the comparative frequency of patches on minute females carrying a lethal and on controls not carrying it. If the frequency of spots on females with a lethal is significantly lower than on the control females, it is assumed that this lethal is a cell-lethal.

It was known at the time of this experiment that such somatic segregation is stimulated by any *X*-chromosome minute. A minute present in the blond translocation was used in this work thus making it easy to introduce into females the lethal to be tested. In the blond translocation, the tips of the first chromosome and the second chromosome are interchanged. If a blond female heterozygous for the translocation is mated to a normal male, about 25 per cent of the female offspring will receive a first chromosome with a translocated second chromosome piece and two normal second chromosomes. Such females will have the end-piece of one of the first chromosomes missing, will have a minute phenotype and will show frequent patches. The procedure adapted in these tests is shown below:

Cross: *dl*–49, *y Hw/l*; +/+ ♀ × Bld^{-1L+2R}; 2^{-2R+1L}/+ ♂

♀ Offspring:
(1) *dl*–49, *y Hw*/Bld^{-1L+2R}; +/2^{-2R+1L} = blond, hairy wing
(2) 1/Bld^{-1L+2R}; +/2^{-2R+1L} = blond
(3) *dl*–49, *y Hw*/Bld^{-1L+2R}; +/+ = blond, hairy wing, minute
(4) 1/Bld^{-1L+2R}; +/+ = blond, minute

When a lethal was located in the middle of the chromosome *dl*–49, *yHw* was used as a balancer and as a marker for the chromosome not carrying the lethal; bar was used when a lethal was located in the left-hand end of the chromosome. Mosaic patches were frequent on minute females (3) and (4), (3) serving as controls and (4) as tests. A significantly lower number of patches on (4) females indicated that the lethal tested was a cell-lethal.

When this experiment was almost completed Stern's[4] finding that autosomal minutes also increase the frequency of somatic segregation of the *X*-chromosome became known to me. In that case twin patches are produced on minute flies; one patch representing the cell lineage of one of the *X*-chromosomes and the other the cell lineage of the other *X*-chromosome. If the lethal to be tested is present in one of the *X*-chromosomes and that lethal is a cell-lethal, only one patch will appear where two are expected, and if the lethal is not a cell-lethal, both of the patches will develop. Since this method is more clear cut and, therefore, more dependable than the previous one, some of the lethals were retested by it as a check on the blond-method. The test made with the autosomal *M* method confirmed the results obtained with blond. The procedure followed with the autosomal *M* method is as follows:

Cross: *dl*–49, *y Hw/y l*; +/+ ♀ × *sn*; M_6/+♂

♀ Offspring: (1) *dl*–49, *y Hw/sn*; +/+ = hairy wing

(2) *y l/sn*; +/+ = wild-type

(3) *dl*–49, *y Hw/sn*; +/M_6 = hairy wing, minute

(4) *y l/sn*; +/M_6 = wild-type, minute

The females listed under (4) were examined and if twin spots (yellow and singed) were found, that indicated that the lethal was not a cell-lethal.

To avoid any misunderstanding it seems advisable to define the term "cell-lethal" as used here and in other papers. This term stands for a lethal which, when homozygous, prevents the appearance of a small patch of tissue for which the test is made. The term does not imply that the lethal in question has a lethal effect on a single cell. In these experiments tests were made on the hypodermal cells of females. It is possible that some of the lethals which are found to be cell-lethal in these cells are not cell-lethal in some other tissue. An example of that type is available in case of the $(y\ ac\ sc)^{-260-1}$ deficiency[5] which is cell-lethal in the hypodermal cells of females but as indicated by the work of Ephrussi[6] is not cell-lethal in the hypodermal cells of males.

Results.—In table 1, 24 lethals are listed 5 of which were tested by both methods. Ten of them were found to be cell-lethal for the hypodermal cells of females.

Discussion.—The finding that about two-fifths of random lethals are cell-lethals differs markedly from the results obtained with lethals affecting known visible loci. In addition to the loci *w, fa, ct, t-amx, m, wy-s, g-ty, Mo-f, f, B+, Bx, M* and *Mn* mentioned in an earlier paper[7] *y-ac* and *dy* have been subsequently tested and should be added to the list. Out of the lethals involving any of these 15 regions of the chromosome, only the lethals for two regions (*y* and *ct*) were found to be non-cell-lethal. While the proportion of cell-lethals to non-cell-lethals for the random lethals was 10 to 14, this proportion for lethals affecting known loci was 13 to 2. Non-cell-lethals affecting visible loci are, therefore, five times as frequent as among random lethals. Visible loci for which lethals were present in these experiments were not selected for any special characteristic. Those were

TABLE 1

RESULTS OF CELL-LETHAL TESTS OF VARIOUS LETHALS

NO.	LETHAL	NO. OF PATCHES CONTROL	NO. OF PATCHES TEST	BLOND METHOD PERCENTAGES OF PATCHES ON M FLIES CONTROL	TEST	DIFFERENCE	D/P. E.	M_0 METHOD PATCHES TWIN	SINGLE
		Cell-lethals							
1	253– 2	67	10	16.1 ± 1.2	3.3 ± 0.7	12.8 ± 1.4	9.2	..	..
2	–12	21	3	12.1 ± 1.7	1.4 ± 0.6	10.7 ± 1.8	6.1	..	..
3	–13	14	4	14.9 ± 2.5	2.9 ± 1.0	12.0 ± 2.7	4.5	..	..
4	–23	..	..	.....	.....	.....	..	..	4
5	–35	..	..	.....	.....	.....	..	..	6
6	–38	14	6	14.0 ± 2.3	4.9 ± 1.3	9.1 ± 2.7	3.4	..	4
7	–40	14	3	13.1 ± 2.2	2.4 ± 0.9	10.7 ± 2.4	4.5	..	..
8	–43	16	4	14.8 ± 2.3	2.9 ± 1.0	11.9 ± 2.5	4.8	..	..
9	–44	21	3	13.6 ± 1.9	2.6	11.1	..	..	..
10	–55	21	9	12.4 ± 1.7	5.26 ± 1.2	7.1 ± 2.1	3.5	..	4
		Not cell-lethals							
11	– 3	19	22	10.9 ± 1.6	11.1 ± 1.5	.....	...	..	..
12	–14	..	..	.....	.....	.....	..	4	..
13	–16	12	14	8.5 ± 1.6	7.1 ± 1.2	1.4 ± 2.0	0.7	..	..
14	–17	..	..	.....	.....	.....	..	4	..
15	–18	15	20	13.2 ± 2.1	13.8 ± 1.9	0.6 ± 2.3	0.2	..	..
16	–19	4	8	10.8 ± 3.4	16.0 ± 3.5	.....	..	4	..
17	–25	..	..	.....	.....	.....	..	4	..
18	–27	6	6	11.5 ± 3.0	10.2 ± 2.7	1.4 ± 4.0	0.4	..	..
19	–28	14	13	8.4 ± 1.5	6.0 ± 2.0	2.4 ± 1.8	1.3	..	..
20	–29	22	11	13.1 ± 1.8	16.2 ± 3.0	3.1 ± 3.5	0.9	3	..
21	–39	..	..	.....	.....	.....	..	6	..
22	–42	..	..	.....	.....	.....	..	3	..
23	–52	10	17	18.9 ± 3.6	25.4 ± 3.6	6.5 ± 5.1	1.3	5	..
24	–51	23	17	16.0 ± 2.1	10.5 ± 1.6	5.5 ± 2.6	2.1	..	..

used for which favorable stock combinations were available at the time of the experiment. They may be taken as representing a random sample of visible loci.

The lethals affecting visible loci are small deficiencies which include in the majority of cases one known locus only. Cytological studies of salivary chromosomes made on a number of these deficiencies show that each of them involves several bands. If each of the bands represents a locus, that suggests that each of these deficiencies involves in addition to the known visible locus several other loci. There is no reason to believe that random lethals are any different from lethals affecting known loci. Probably all or at least a great majority of them are deficiencies. If these lethals are deficiencies, there is again no reason to suppose that they are different from those affect-

ing known loci since both were produced by the same agent. It seems justifiable to assume, therefore, that these two sets of lethals are comparable except for the fact that in one case a known locus is involved and in the other case either no known locus is affected or if it is that fact has not been discovered. If this assumption is granted, the unavoidable conclusion is that the difference in the proportion of cell-lethals observed in these sets is due to the presence in one of deficiencies affecting known visible loci. This would indicate, that, on the average, loci in which genic changes have a visible effect play a more important rôle in the vital processes of an organism that the loci in which genic changes do not show such an effect. As has been mentioned elsewhere[8] there is ample evidence pointing to such a difference between various loci. In some instances, as in the case of notch (facet) and several minutes, a heterozygous deficiency has a striking upsetting effect upon the organism, while in another case a homozygous deficiency involving four bands of the tip end of the *X*-chromosome and presumably involving at least four loci is perfectly viable.

Summary.—Out of the 24 *X*-chromosome lethals produced at random by *X*-rays 10 were found to be cell-lethal in the hypodermal cells of females. These lethals are compared with lethals affecting known visible loci in which 13 out of 15 were found to be cell-lethals. The higher frequency of cell-lethals among lethals affecting visible loci suggests that on the average these loci play a more significant rôle in the vital processes of the organism than do the other loci.

An opinion is expressed that the majority of lethals are probably deficiencies.

[1] Demerec, M., these PROCEEDINGS, **20**, 354–359 (1934).

[2] The following symbols are used in this paper: *ac* = achaete; *amx* = almondex; *B* = bar; *Bld* = blond; *Bx* = beadex; *ct* = cut; *dl*–49 = delta–49 inversion; *dy* = dusky; *f* = forked; *fa* = facet; *g* = garnet; *Hw* = hairy-wing; *l* = lethal; *m* = miniature; *M* = minute; *Mn* = minute-n; *Mo* = minute-o; M_6 = minute-6; *s* = sable; *sc* = scute; *sn* = singed; *t* = tan; *ty* = tiny; *v* = vermilion; *w* = white; *wy* = wavy; *y* = yellow; 1 = first chromosome; 2 = second chromosome; + = wild-type.

[3] Bridges, C. B., these PROCEEDINGS, **11**, 701–706 (1925).

[4] Stern, C., *Amer. Nat.*, **68**, 164–165 (1934); *Ibid.*, **69**, 81–82 (1935).

[5] Demerec, M., and Hoover, M., *Amer. Jour. Hered.*, **27**, 206–212 (1936).

[6] Ephrussi, B., these PROCEEDINGS, **20**, 420–422 (1934).

[7] Demerec, M., *Cold Spring Harbor Symposia on Quant. Biol.*, **2**, 110–115 (1934).

[8] Demerec, M., *Science*, **81**, 420 (1935).

PUBERTY IN ESKIMO GIRLS

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Mrs. Lulu Heron, for many years now the Government Nurse to the Eskimos of the Lower Kuskokwim River, Alaska, with the aid of Miss Ann Martin, teacher in the Government School at Bethel, has kindly gathered for me, since my visit to the region in 1930, the following records on the setting in and some characteristics of the menstruation in 16 full-blood and 6 mixed (Eskimo-white) girls.

NAME	FULL BLOOD	MIXED BLOOD	AGE	BEGAN TO MENSTRUATE	AVERAGE DURATION DAYS	CHARACTERISTIC FEATURES	REGULARITY
E. Hawk	x		14*	7-19-28	5 2/3	Painless	Regular
F. Otto	x		12	5-20-30	4 2/3	Painful first day	Regular
L. Jordan	x		14	8-4-30	4 2/3	Slight discomfort	Regular
Annabelle	x		13	6-15-30	5	Slight pain	Irregular
Elsie S.	x		12	12-1-31	4 1/2	Normal	Irregular
Alice K.	x		13	12-20-31	7 to 8	Painful	Irregular occasionally
Julia F.	x		13 1/2	2-6-28	4	Painless	Regular
Elena J.	x		14 6/12	4-24-35	3 1/2	Painless	Reg., every 21 days
Fanny B.	x		14 2/12	5-28-33	4 or 5	Pain first day	Regular
Annie K.	x		13	9-15-34	3	Some pain	Regular
Julia S.	x		14	2-26-29	5	Slight discomfort	Irregular occasionally
Mary Greg	x		13	6-6-25	3 1/2	Painless	Irreg., approx. every 3 wks.
Marie T.	x		14	1-19-33	5	Painless	Regular
Elsie M.	x		13	12-24-35	5	Some pain	Regular
Elena Waska	x		12	12-20-29	4	Painless	Regular
Elsie N.	x		14	6-4-35	6	Pain first day	Regular
Means			13.3+	near	4 3/4		
E. Liskey		x	13	5-21-32	3 1/2	Painless	Regular
Ellen H.		x	15			Painful	Irregular
Gladys H.		x	14	7-30-30	5	Painless	Regular
Helen J.		x	11	12-17-32	5	Painless	Regular
Mary J.		x	13	2-4-28	4	Painful at times	Regular
Mary Alice S.		x	13	7-25-35	8	Cramps on 2nd day	Regular
Means			13.2+		4 1/4		

* Passed or close to.

The above records may be regarded, I think, with full confidence. Mrs. Heron is a trained, eai nest nurse and was well aware of the need for accuracy. The only defect of the data is that, barring few exceptions, the age is not given to months, and that possibly a small minority of the "full-blood" subjects may have had a trace of old white admixture. Judging from the showing of the mixed-bloods, however, such a slight admixture would have had no effect on the function under consideration.

The observations were all made at Bethel, but the parents of the girls and even themselves may have come from any of the native villages along the river.

The Kuskokwim Eskimos belong to the largest, best preserved and least admixed groups of this people. The subjects were schoolgirls, living under fairly civilized but by no means modern city conditions. The principal food of their parents as well as themselves was fish, supplemented somewhat by bread and other white man's articles, with but little meat. The land in the Bethel region is all less than 100 feet above sea level, the climate is subarctic, with considerable moisture in summer.

The records show a number of points of interest. The age of onset of menstruation of approximately $13^1/_2$ years for both groups[1] is unexpectedly low for so far north. It does not differ appreciably in the full- and the mixed-bloods, so far as these records go. The main seasons of incidence were the summer months, and again the winter months; no case began in March, October or November. In one half of both the full-blood and the mixed-blood more or less pain attended the function. Its average duration was close to $4^3/_4$ days in full-bloods, $4^1/_4$ days in the mixed-bloods, which is closely similar.

Former knowledge on the age of puberty among the Eskimo girls had been gathered by Weyer,[2] whose data may here be quoted in full:

"Berthelsen determined that the average age at the time of the first menstruation was fifteen years and five months among 127 women in the Umánaq District, some of whom were of mixed parentage. Of the total, forty-two are put down as being of pure Eskimo race, and for them the average was fifteen years and six months. Another determination of the age of Greenland girls at their first menstruation, based on one hundred individuals, is cited by Ploss on the authority of Von Haven as follows: 88 girls between the ages of 15 and 17; 5 girls before the age of 15; 7 girls after the age of 17.

"It is written of the Eskimos of Cumberland Sound that 'sexual maturity makes its appearance early, so far as can be learned of a people of whom no one knows his age, even at 13 or 14 years among females.' Lundberg asserts that among twenty-one Labrador Eskimo girls five who were not yet having their monthly periods were fourteen years old or less; of the sixteen others who were already menstruating, the function first appeared between

the ages of fourteen and fifteen in four individuals, between sixteen and seventeen in three, and not until twenty in two cases. The average age thus amounts to about sixteen years. According to MacDiarmid, who accompanied the arctic expedition under John Ross as its doctor, menstruation among the Eskimos often first begins at the age of twenty-three and even then occurs only during the summer months. Again it is stated that Eskimo girls have their first menstruation when between the ages of thirteen and fifteen years. Turner gives thirteen years for the approximate age in Labrador; Kelly's estimate of the age of maturity in Eskimo girls is likewise thirteen years; and according to Dr. Thompson, who has practiced for a number of years among the Eskimos of Alaska, the probable average age, not based upon statistics, is about fourteen years. Stenfansson's attention was directed to the early age of maturity among Eskimo girls by Dr. H. R. Marsh, a medical missionary at Point Barrow, and he estimated the age among western Eskimo girls at from ten to fourteen years."

Speculation as to the causes of the rather early puberty in the so far observed western Eskimo young women, would be premature. The facts can only be determined by careful studies on the heredity, personal environment, nourishment and metabolism in these subjects.

[1] The means, 13.3 for the full-blood and 13.2 for the mixed-blood, should perhaps be augmented a little because in most of the subjects the age was probably something over the year given.

[2] Weyer, E. F., *The Eskimos, Their Environment and Folkways*, **80**, New Haven (Yale Univ. Press), 46–49 (1932).

ESKIMO CHRONOLOGY

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An analysis of the archaeological collections from an extensive Eskimo village site at Kukulik, St. Lawrence Island, Alaska, has shown that six cultural horizons, marked by changes in material culture, are represented in a single stratified midden deposit. A "test cut" excavated through the midden exposed a deposit of refuse with a maximum depth of 14 feet, and in the walls of the trench strata of sod were apparent marking periods in the history of the mound when it had been abandoned and over-grown with grass. Although the mound is only partially excavated and the changes in material culture have not been precisely correlated with the reoccupations of the site indicated by the sod strata, it is clear that at least six cultural periods may be defined.

Since most of the cultural elements which distinguish each of these six periods particularly characterize Eskimo cultures found at other sites in the Arctic region, the stratigraphic relation of these elements at Kukulik has a significant bearing upon the cultural sequence in the Eskimo area.

Excavation of the Kukulik site was begun in 1931 by Otto Wm. Geist for the University of Alaska, and operations were continued until the fall of 1935. During the last two seasons (1934–35) the work, with Mr. Geist in charge, was conducted as a Public Works project under the auspices of the U. S. Department of the Interior, Bureau of Indian Affairs and the University of Alaska.

The collection resulting from these excavations has been estimated at approximately 50,000 artifacts. The large part of this collection was obtained during the seasons of 1934 and 1935 when the entire surface of the eastern end of the midden was cut down approximately 36 inches. Most of the house and meat cache structures found in this upper level of debris, in addition to native artifacts, contained numerous iron tools, glass beads and bottles, hard wood fragments and other objects which could have been obtained by the Eskimo only through extensive trade with modern ships. Thus most of the collection represents a relatively recent Eskimo culture, not unlike that still functioning on St. Lawrence Island. However, in 1931–32–33 a test cut 30 feet wide, 135 feet long and extending to the base of the deposit was excavated through the midden and in 1934–35 deep cuts were made along the beach slope where the surf was encroaching on the mound. The stratigraphic analysis has been limited primarily to the objects found in these sections of the midden, but material from the general surface level has been used to determine the entire cultural complex of the most recent phase. A summary of each cultural period may be given as follows:

Modern.—In the winter of 1879–80 a famine on St. Lawrence Island destroyed a large part of the population, and Dr. E. W. Nelson has informed Mr. Geist that Kukulik was in all probability one of the abandoned sites which he visited shortly after the famine, where he found the houses filled with the dead. Since the site, therefore, was apparently occupied as late as 1879 and since the material from most of the structures on the surface of the mound contained a large number of modern trade objects, the cultural period represented by this material has been termed "Modern." The depth of the Modern level is indicated in the test cut by a large house structure which extended to a depth of 4 feet.

This last, or Modern, phase of occupation is particularly characterized by bone and ivory harpoon heads (type *A*) with a closed socket, a blade slit parallel to the axis of the line hole and a single spur, a type of harpoon head used throughout a large part of the Eskimo area during modern times.[1] Decorated ivory objects are conspicuously absent. Most of the

associated bone, ivory, wooden, baleen and stone artifacts obtained in these Modern structures are remarkably like those which characterize the prehistoric Thule culture in the eastern Arctic.[2]

Recent-Prehistoric.—Under the Modern house in the test cut lay a second house structure with the floor six feet below the surface. The majority of artifacts from this structure resemble those obtained in the house above, and correlate similarly with the Thule types. Most of the harpoon heads found in the second house, however, are a distinct type (*B*) which is notably different from the Modern type *A*. These type *B* heads, with a single spur and a blade slit parallel to the round-to-triangular line hole, have an open rather than a closed socket without slots or holes for foreshaft lashings, and are flat rather than oval in cross-section. Harpoon heads of this type were found in various sections of the midden directly below Modern structures.

A third house structure, the floor of which lay nine feet below the surface in the test cut, appeared below the second house but not clearly separated from it, since the second appeared to be a rebuilding of the third after this had filled in with debris. Although the material from the third house is obviously older than that from the second, the same type of harpoon (*B*) predominates in both and there are no significant variations in other artifacts. An awl and a knife blade made of wrought iron and a button-like object of lead were found in the second house, while a single wrought iron knife blade was found in the third. The presence of these implements and the absence of any other objects which might be derived from modern trade leaves some question as to the age of these deposits. The metal objects in the second house may have been obtained through early Russian trade, but the iron knife in the third house, if actually "*in situ*," would probably indicate prehistoric trade with some native people of Siberia in possession of iron, since it is unlikely that nine feet of deposit could accumulate between the time of Russian contact and the desertion of the site in 1879. In any case the material from the second and third houses, since it is characterized by the type *B* harpoon head, differs significantly from the Modern house material and marks a particular phase of occupation which has been termed "Recent-Prehistoric."

Thule.—Below the third house in the test cut the stratigraphic study has been based on a limited number of precisely located specimens, as collections adequate for this purpose could not be associated with particular house structures. Directly below the third house, between the depths of 9′ and 10′ 6″, two types of harpoon head (*C* and *8*) predominated. These types are characteristic of the Thule Culture sites in the eastern Arctic and have been defined by Mathiassen[2] as "Thule types 2 and 3." The other artifacts definitely located in this level are not sufficient in number for a comparison with those from the house structures above.

A meat cache structure (No. 35), discovered in 1935 at a depth of 5 feet in the eastern end of the mound, lay directly below Recent-Prehistoric structures and contained harpoon heads which are also clearly "Thule types." Three are the "Thule type 3," two are the "Thule type 2," and two are very closely related to the "Thule type 1." The associated artifacts are, as a whole, the same as those from the three house levels in the test cut. "Thule type" harpoon heads were also found at depths of from four to six feet below Recent-Prehistoric refuse in the beach slope cut.

The presence, in three different sections of the mound, of "Thule type" harpoons in strata below Recent-Prehistoric type *B* quite certainly represents a "Thule phase" at Kukulik. Only one of these sections (meat cache No. 35) produced an adequate collection of associated artifacts. These are also "Thule types."

Punuk.—Three types of harpoon heads (*D*, *E* and *F*) found in the test cut below "Thule types" and between the depths of 10′ 6″ and 12′ 3″, are incised with decorations of the "Punuk style" which particularly characterizes a "Punuk Culture" discovered by H. B. Collins[3] at sites on Punuk and St. Lawrence Islands. These harpoons, numbering ten specimens, are not distinctive in form, since *D* specimens are similar in shape to *C* (Thule type 3) and *E* specimens are similar to the Modern *A* harpoon heads. They are classed as separate types primarily because of the incised decorations which are simple patterns of converging lines, *Y* figures, spurs and punctures. Twenty specimens of the same types (*D*, *E* and *F*) were found below "Thule types" in the beach slope cut at depths ranging from 6 to 11 feet. No adequate collection of other artifacts has been obtained from these levels in the deposit, but several implements decorated in the "Punuk style" were found associated with the harpoon types *D*, *E* and *F* in both deep cuts. Some of these objects are decorated with the "late Punuk," while all of the harpoon heads are decorated in the "early Punuk" pattern, as defined by Collins.[3] This distinction is essentially based upon the appearance of precise "compass-made" circles on objects found in late Punuk deposits at Gambell, St. Lawrence Island.

Birnirk.—Two types of harpoon heads (*G*, *H*) found in the lower levels of the deposit are very similar to the harpoons which predominate at the Birnirk site near Point Barrow,[4] Alaska, and also in the Van Valin collections[5] from Point Barrow. The *G* type heads have side cutting blades parallel to the line hole, an open socket and a bifurcated spur. Most of the specimens are made from bone, unlike other harpoons at Kukulik which are normally ivory, and the cutting blades are made from shells. The *H* type heads have side cutting blades at right angles to the axis of the line hole, an open socket and a trifurcated spur. Most of them are also made from bone, but the side blades are usually flint. Harpoon heads of both types are occasionally incised with simple straight lines

running the length of the head on both sides of the line hole. Seven of these "Birnirk type" harpoons are definitely located in the test cut and nine in the beach slope cut, but a large number have been found in various sections where stratigraphic relationship of types is not clear. Field notes state that "Birnirk types" when "*in situ*," always appear associated with sod-strata which are older than the sod-strata with which "Punuk types" are associated, but a definite correlation of sod-strata with the various types has not yet been possible, and the stratigraphic charts leave some question as to the relative age of these two types. However, relying upon the field notes, a "Birnirk phase" at Kukulik may be recognized.

Old Bering Sea.—Three types of harpoon heads (*I*, *J* and *K*) and a number of other implements found on or within a few inches of sterile clay at the base of the midden are incised with decorations of the "Old Bering Sea Style" as described by Jenness,[1] Hrdlička,[6] Collins[3] and Mathiassen.[7] This style of decoration particularly characterizes the "Old Bering Sea Culture" discovered by Collins[3] at Gambell, St. Lawrence Island. The forms of the "Old Bering Sea harpoon types" at Kukulik are not distinctive, since *I* specimens are like *F* specimens (Punuk) and type *J* is similar to type *H* (Birnirk). The types are distinguished principally on the basis of the incised decorations which are made up of elaborate curvilinear design elements, bosses punctured at the center and outlined by incisions, zoömorphic heads in low relief outlined by incisions, and petaloid elements.

Six of the "Old Bering Sea type" harpoons were found at the base of the deposit (13 to 14 feet deep) in the test cut, and seventeen within 2 feet of sterile clay in the beach slope cut. Among the implements other than harpoons decorated with the "Old Bering Sea" design are several winged "ceremonial" objects similar to others found in the Bering Sea region and previously described.[3] These objects, like the somewhat similar wedge-shaped "ceremonial" specimens found in a more recent level at Kukulik associated with "Punuk type" harpoons, are of conjectural use and unknown to the modern Eskimo. Other objects found in the lowest level of refuse are essentially Eskimoid in character, and many are types which are the same as, or very similar to, those found throughout all levels in the midden, but specimens with the "Old Bering Sea type" of decoration are, apparently, limited to the lowest level of refuse. Above this the field notes record the presence of an "Old Bering Sea sod-stratum" marking the termination of the first period of occupation at Kukulik.

Conclusions.—The six cultural horizons observed in the Kukulik midden have been determined by a change in particular cultural elements only. Styles of decoration characterize the Old Bering Sea and Punuk periods, while distinctive types of harpoon heads characterize the Birnirk, Thule, Recent-Prehistoric and Modern. The last three periods (Thule, Recent-

Prehistoric and Modern) appear to be stages in the development of a "Thule Culture complex." These stages are marked primarily by a change in the form of harpoon heads, since most of the other artifacts found in the three upper levels of refuse are the "Thule types" as defined by Mathiassen. With the limited number of specimens obtained from the lower levels it is not possible to determine the entire complex of characterizing elements nor the extent of the cultural change which occurred during the Old Bering Sea, Birnirk and Punuk periods. That objects Eskimoid in type are found throughout the entire deposit is, however, clear. Many of these types have a wide distribution in the Arctic area, and future excavations in the lower refuse levels at the site, together with a detailed study of the relation between Kukulik and other sites in the Arctic region, will undoubtedly make it possible to estimate the extent of the cultural changes which took place, and to determine whether these were due to local development, to immigration of new peoples or to contact with distinct cultures in the Eskimo area.

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[2] Mathiassen, Therkel, "Archaeology of the Central Eskimos," *Rept. Fifth Thule Expedition*, 1921–24, **4**, Copenhagen (1927).

[3] Collins, Henry B., "Archaeology of the Bering Sea Region," The Smithsonian Report for 1933, 453–468, Washington, D. C. (1935).

[4] Wissler, Clark, "Harpoons and Darts in the Stefánsson Collection," Anthropological Papers of the *Am. Mus. Natl. Hist.*, **14**, pt. II, New York (1916).

[5] Mason, J. Alden, "Excavations of Eskimo Thule Culture Sites at Point Barrow, Alaska," *Proc. 23rd. Internatl. Cong. Americanists*, New York, 1928. N. Y. (1930).

[6] Hrdlička, Aleš, "Anthropological Survey in Alaska," *46th Ann. Rept. Bur. Ethnology*, Washington, D. C. (1930).

[7] Mathiassen, Therkel, "Some Specimens from the Bering Sea Culture," *Indian Notes*, **6**, No. 1, *Mus. Am. Indian*, Heye Foundation, N. Y. (1929).

TORSION OF RECTANGULAR TUBES[1]

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The problem of determining the stresses in prismatic bars subject to a twisting moment was solved by Saint-Venant. Lord Kelvin pointed out a hydrodynamical analogy and Prandtl developed a membrane analogy, rigorously correct for solid bars of simple section as well as for tubes of circular section and greatly facilitating an approximative solution. The hydrodynamical analogy was extended by R. Bredt[2] to thin-walled rec-

tangular tubes, and it is with the theory in that form that the present paper is particularly concerned.

According to this theory the shearing stresses are conceived to behave in the manner of an ideal fluid, flowing with constant rotation around the tube between the inner and outer contour of the walls. The product of the stresses and the thickness of the walls at any point is constant. If the walls are of uniform thickness, the stresses are the same everywhere except quite locally at the reëntrant corners, where higher stresses exist and at the external edges where the stresses are known to be zero. It is also conceded that a minor difference exists between the stresses on the external and internal surfaces, but the variation is assumed to be linear

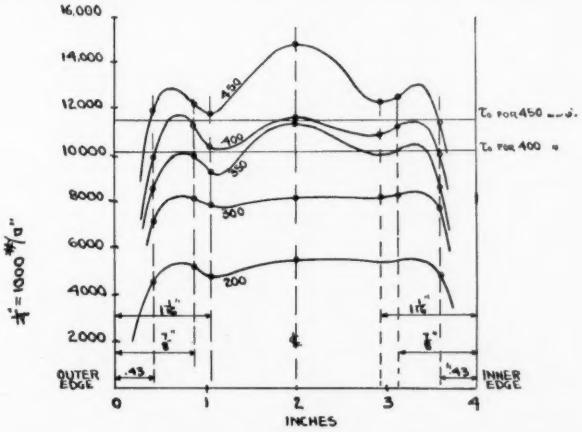

FIGURE 1

Tube "*E*"—4″ × 4″ × 3/16″. Curves of shearing stress external surface, top wall Feb. 21 and 25, 1936.

across the thickness, so that the shearing stress at the middle surface can be used as a generalized stress acting uniformly in the walls all around the tube.

The solution is admittedly an approximation, but it rests on a correspondence between the fundamental equations for the stresses in the Theory of Elasticity and those for the velocities of a perfect fluid in the Theory of Hydrodynamics. In fact, one set of equations can be obtained from the other by multiplication with a simple factor.

Place an XY-system of coördinates in a transverse section of the tube with origin at the axis, let τ_x and τ_y be the component shearing stresses and ϑ the angle of torsion. The normal stresses and τ_z are assumed to be zero.

Then the stress equation for equilibrium is:

$$\frac{\partial \tau_y}{\partial x} + \frac{\partial \tau_x}{\partial y} = 0 \tag{1}$$

and the distortion of the tube is expressed by:

$$\frac{\partial \tau_y}{\partial y} - \frac{\partial \tau_x}{\partial x} = -2G\vartheta = \text{constant.} \tag{2}$$

Let the generalized or mean stress be τ_0 and regard it as a vector with the components τ_x and τ_y, then, according to Stoke's Theorem:

$$\int\int \left(\frac{\partial \tau_y}{\partial y} - \frac{\partial \tau_x}{\partial x}\right) dx\, dy = \int \tau_0\, ds \tag{3}$$

and hence:

$$\int \tau_0\, ds = 2G\vartheta A \tag{4}$$

where A is the area of the section of the tube comprised within the middle contour of the walls.

Let t be the thickness of the walls, here assumed to be constant all around the contour, and T the twisting moment, then it follows from statics that:

$$\tau_0 = \frac{T}{2At} \tag{5}$$

and hence from (4), the angle of torsion is:

$$\vartheta = \frac{TS}{4A^2Gt} \tag{6}$$

where S is the total length of the middle contour.

The simple equations (5) and (6) give the whole solution for tubes of uniform thickness, and being built up from the fundamentals of the Theory of Elasticity they have an unusual degree of plausibility. The beauty of the hydrodynamical analogy and the simplicity of the equations probably account for the fact that this solution has been generally accepted by engineers. It appeared to the author, however, that there were at least two reasons for questioning its correctness. First, in a solid rectangular section the stress lines, even close to the contour, are not rectangular and the flow of the stresses is quite different from the uniformity assumed for rectangular tubes. In fact, the stresses have a maximum at the middle of the four sides. Second, the stress concentration at the reëntrant corners, which causes the plastic condition to be reached at an early stage when a torque is applied, disturbs the analogy with a friction-

less fluid. An analogy may exist, however, with the flow of an ordinary fluid, since in such a case the viscous forces bear a relation to the velocities quite similar to that which the forces of restitution in an isotropic solid bear to the displacements.[3]

The only previous experiments on the torsion of rectangular tubes, known to the author, were those made in 1923 by Mr. George Vedeler.[4] Three very thin-walled tubes were tested; the angle of torsion was observed, but no strain measurements were made. It appears that the tubes failed by buckling. The results did not agree with formulas (5) and (6),

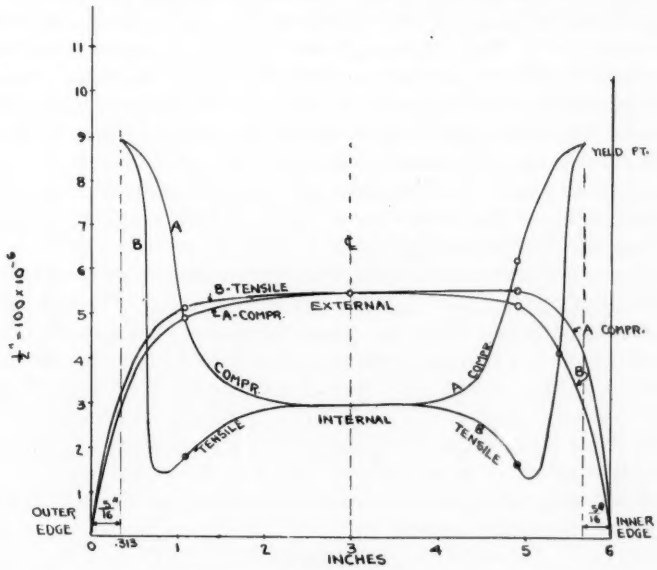

FIGURE 2

Tube "D"—$6'' \times 3'' \times {}^{5}/_{16}''$. Curves of strains: bottom wall, internal and external. $W = 700$ lbs.

and Vedeler concluded that the ratio between the sides of the rectangular section had a strong influence on the stiffness of the tubes.

In order to study this problem in more detail, the author made a number of tests in which not only the angle of twist but also the strains were measured. Altogether five tubes of mild steel were tested, one of which was built up of four plates welded together at the corners, and four were drawn. The tubes will be referred to as A, B, C, D and E. Strains were measured on C, D and E. The tests were made in the Material Laboratory of the New York Navy Yard.

As no torsion testing machine was available, it was necessary to improvise a special mechanism. The tube to be tested rested on bearings at the ends and was welded to two parallel arms of which one was held in a fixed horizontal position, being attached to the short lever of a testing machine, while the other was forced down by a turnbuckle. The force exerted on the fixed arm being measured, the twisting moment could be calculated.

Two pointers near the ends of the tube permitted an exact determination of the torsional angle, and Huggenberger tensometers were employed to measure the strains. In pure torsion the principal stresses, σ_1 and σ_2, act at 45 and 135 degrees to the axial direction, whence most of the strains were measured at those angles. On the external surface of the tubes σ_1 was always numerically equal to σ_2 so that the shearing stress was equal to the measured principal stress. Strains were also measured in directions parallel with and normal to the axis, and were always found to be practically equal to zero, as might be expected.

On tube D strains were measured not only externally, but also on the internal surface of the lower wall by means of a scissor-like device which was inserted through holes in the upper wall.

The external stress distribution across a transverse line in the E-tube is shown in figure 1. It is seen that the mean theoretical shearing stress, τ_0, is considerably lower than the measured maximum stress on the external surface, but it is a matter of still greater importance that breakdown of the tubes occurred when τ_0 was much lower than the yield point in shearing τ_f, which is taken at 0.577 times the yield point in tension, σ_f. The stresses have a maximum at the center line and moreover, maxima exist in this tube on each side at some distance from the edges.

The following table gives the principal data for the tubes C, D and E and the stresses at breakdown.

TABLE 1

TUBE	DIMENSIONS OF TUBE INCHES	YIELD POINT IN TENSION σ_f LBS./SQ. IN.	YIELD POINT IN SHEARING τ_f LBS./SQ. IN.	MEAN SHEARING STRESS THEORY τ_0 LBS./SQ. IN.	MAXIMUM SHEARING STRESS MEASURED ON CENTER LINE EXTERNAL τ_{max} LBS./SQ. IN.
C	$52 \times 3 \times 3 \times .070$	24,000	13,900	10,000	12,700
D	$51 \times 3 \times 6 \times .313$	35,500	20,500	10,540	12,300
E	$51 \times 4 \times 4 \times .192$	26,000	15,000	10,350	11,680

All these tubes were of mild steel, drawn and annealed.

Figure 2 gives curves for the internal as well as the external strains at a number of points on the lower wall of the $3'' \times 6''$ tube, D. At the center-line the external stress is 12,650 lbs. per sq. in. as compared with an internal stress of 6900 lbs. per sq. in. and great irregularities exist in the distribution of the internal stresses near the reëntrant corners.

Strain lines on the external surface appeared first near the edges with which they ran nearly parallel.

Judging from these experiments, the shearing stresses in rectangular tubes are distributed in a very irregular manner, quite different from that assumed in the hydrodynamical analogy. Some regions, located on the internal surface of the walls, are very low-stressed at the point of breakdown, so that other regions must be stressed very highly since the mean stress for the whole section must be equal to τ_0 in order to balance the twisting moment.

The observed angle of torsion showed in all cases a very close agreement with theory, a fact which may be explained by the equalizing or, it may be said, generalizing tendency of the tube as a whole, since the stresses, although distributed in a highly uneven manner, yet have to balance the applied twisting moment. In fact, the twist of the whole tube is an expression of the integral effect of all the local and highly variable distortions, and thus the total torsional stiffness may not be materially affected.

Hence the accepted theory, by representing the angle of torsion correctly up to the point of breakdown, while giving an incorrect picture of the stress distribution, is deceptive and may in some cases lead to a dangerous underestimate of the stresses.

[1] The work on which this report is based was carried out under the authority of the Bureau of Yards and Docks and with the permission of the Bureau of Construction and Repair of the U. S. Navy Department in the Material Laboratory of the New York Navy Yard in 1935–1936.

[2] A. and L. Föppl, *Drang und Zwang*, pp. 80 and 128 (1920).

[3] Lord Rayleigh, *Theory of Sound, II*, p. 314 (1926).

[4] "On the Torsion of Ships," *Trans. Inst. Nav. Arch.* (1924).

ON THE PROBLEM OF PLATEAU

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The solution of Plateau's problem has recently been the subject of a series of important papers by Garnier, Douglas, Radó, McShane and others.[1] The first complete general proofs for the existence of a minimal surface with a single given Jordan curve as boundary were published independently by Radó and Douglas at about the same time.[2] Douglas later has attacked the problem with the much more general aim of establishing the existence of a minimal surface bounded by k given Jordan curves and having a prescribed topological structure. He has announced a complete result and

has so far published the solutions for the case $k = 1$, $k = 2$ when the topological type is respectively that of a circle, an annular ring or Möbius strip. His method is based upon the discussion of a functional giving the value of the Dirichlet integral of a potential function through its boundary values on a circular domain. The proof is striking by its bold departure from classical lines and by significant explicit expressions. However, the desire to understand Douglas' theory from a more conceptional and classical point of view has resulted in an existence proof the outlines of which are given in the following pages.[3] This proof furnishes the solution of the problem in a simple way with complete generality as far as the topological structure of the minimal surface is concerned. Moreover, it also covers the case when parts of the boundaries are free to lie on prescribed surfaces.

1. *Statement of the Problem.*—A minimal surface in the n-dimensional space of the vector $\mathfrak{x}$ with the coördinates $x_1, \ldots, x_n$ is defined as one capable of a parametric representation $\mathfrak{x}(u, v)$ in terms of two parameters u,v so that in the corresponding u,v-domain $\Delta\mathfrak{x} = \mathfrak{x}_{uu} + \mathfrak{x}_{vv} = 0$ and $\mathfrak{x}_u\mathfrak{x}_v = 0$, $\mathfrak{x}_u^2 - \mathfrak{x}_v^2 = 0$. The problem is to prove the existence of such surfaces bounded by k prescribed Jordan curves $\Gamma_1,\Gamma_2, \ldots, \Gamma_k$. The solution will appear as solution of the following minimum problem.

Problem I. Let G be any domain in the u,v-plane bounded by k circles $C_1, \ldots, C_k$. Let $\mathfrak{x}(u,v)$ be a vector continuous in G and on its boundaries, such that $\mathfrak{x}$ maps $C_1, \ldots, C_k$ in a continuous and monotonic way into $\Gamma_1, \ldots, \Gamma_n$ and that the Dirichlet integral over G

$$D(\mathfrak{x}) = \int\int (\mathfrak{x}_u^2 + \mathfrak{x}_v^2)dudv$$

exists. We ask for a domain G and in it a vector $\mathfrak{x}$ so that $D(\mathfrak{x})$ has the smallest possible value d.

Since $D(\mathfrak{x})$ is invariant under conformal mapping we may add, without changing the values of $D(\mathfrak{x})$, any kind of conditions which replace G and $\mathfrak{x}$ by conformally equivalent domains and vectors.

2. *Solution of Problem I.*—Let d be the lower limit of $D(\mathfrak{x})$ and $\mathfrak{x}_1$, $\mathfrak{x}_2$, ... a minimizing sequence of admissible vectors; $D(\mathfrak{x}_n) \longrightarrow d$, G_1, G_2, ... the corresponding sequence of domains. We may assume that $\mathfrak{x}_n$ is a potential vector in G, $\Delta\mathfrak{x}_n = 0$; for otherwise we could replace it by a potential vector with the same boundary values and smaller Dirichlet integral.

We first consider the case $k = 1$. Here we may suppose that all the domains G_n are identical with the unit circle C and that $\mathfrak{x}$ transforms three given points on the boundary of C into three given points on Γ. We prove: *The boundary values of $\mathfrak{x}$ on C are equicontinuous.*[4] If it were not so we could assume the existence of a positive constant α and two sequences P_n, Q_n of points on C, both converging to the same boundary point R,

such that $|\mathfrak{x}(P_n) - \mathfrak{x}(Q_n)| \geq \alpha$. Let A and B be two arbitrarily fixed points on C with the same distance l from R, b being the arc $\overset{\frown}{AP_nQ_nB}$. Let A_n', B_n', R_n', P_n', Q_n' be the images of A, B, R, P, Q on Γ. Let b_n' be the arc $\overset{\frown}{A_n'R_n'B_n'}$ on Γ and γ_n the complementary arc. Then the following *lemma* holds: *The diameter of δ_n tends to zero as n increases.* Otherwise there would be a positive constant q, for which $\mathfrak{x}_n(P) - \mathfrak{x}_n(Q) \geq q$ whenever P lies in b on P_nA and Q in Q_nB. We introduce polar coördinates r, ϑ around R. Then we consider an arc PQ of a circle with the radius r of this polar coördinate system. We certainly have $q \leq \left| \int_P^Q \frac{\partial \mathfrak{x}_n}{\partial \vartheta} d\vartheta \right|$ and on account of Schwarz's inequality $q^2 \leq \pi \int_P^\vartheta \left| \frac{\partial \mathfrak{x}_n}{\partial \vartheta} \right|^2 d\vartheta$. Now, if

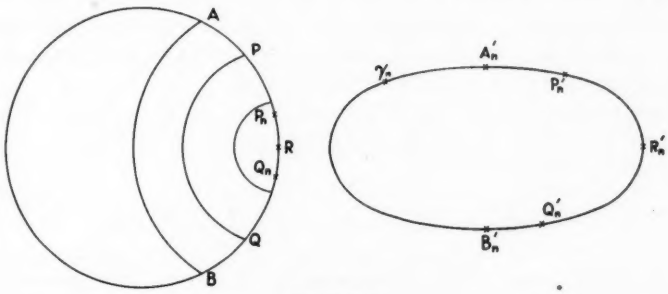

FIGURE 1

n is sufficiently large this holds for all values of r between $r = \epsilon$ and $r = l$, ϵ being chosen arbitrarily small. Multiplying the last equation by $1/r$ and integrating with respect to r between these limits, we obtain immediately

$$q^2 \log \frac{l}{\epsilon} \leq \int_\epsilon^l \int_P^Q \frac{1}{r^2}\left(\frac{\partial \mathfrak{x}_n}{\partial \vartheta}\right)^2 r dr d\vartheta \leq \int_G\int (\mathfrak{x}_u^2 + \mathfrak{x}_v^2)\, du dv = D(\mathfrak{x}_n).$$

Since the right side is bounded the assumption of a positive q contradicts the arbitrariness of ϵ and the lemma is proved. Now the statement in this lemma is incompatible with the three point condition, hence the equicontinuity of the vectors $\mathfrak{x}_n$ is established.

Therefore we can choose a subsequence, again called $\mathfrak{x}_1, \mathfrak{x}_2, \ldots$ which converges uniformly on C, and hence in G toward a potential vector $\mathfrak{x}$, continuous in the closed circle and satisfying the conditions of Problem I. Since in every concentric circle the derivatives of $\mathfrak{x}_n$ converge uniformly to the derivatives of $\mathfrak{x}$ and since $D(\mathfrak{x}) \geq d$ we obtain in the usual way $D(\mathfrak{x}) = d$, i.e., $\mathfrak{x}$ solves Problem I.

In the case $k > 1$ we consider the typical example $k = 2$. The two boundary circles C_1, C_2 of G can be chosen as concentric with radii ρ_1 and $\rho_2 > \rho_1$ of which ρ_1 can be fixed, $\rho_1 = 1$. Setting $\sigma^2 = \rho_1\rho_2$, we modify Problem I into Problem II by adding the condition $\mathfrak{x} = 0$ on the intermediate circle with the radius σ, thus restricting the range of competition. Therefore for the lower bound δ_σ in Problem II we have certainly $d \leq \delta_\sigma$. But, if σ is sufficiently large, one notices easily that δ_σ differs by an arbitrarily small quantity from $d_1 + d_2$, where d_1 and d_2 are the lower limits belonging to the single curves Γ_1 and Γ_2, respectively; hence $d_1 + d_2 \geq d$. With Douglas we exclude the equality sign by requiring

$$d_1 + d_2 > d.$$

Under this condition ρ_2 in the minimizing sequence $\mathfrak{x}_n$ and G_n must remain bounded. Further ρ_2 cannot have 1 as a limit, because this easily is seen to contradict the boundedness of $D(\mathfrak{x}_n)$. Hence we may assume that G_n converges to a concentric annular ring G, and we could have chosen G from the beginning as this fixed annular ring.

Now we again prove: $\mathfrak{x}_n$ is equicontinuous on C_1 and C_2. We put $\mathfrak{x}_n = \mathfrak{y}_n + \mathfrak{z}_n$ where $\Delta\mathfrak{y}_n = \Delta\mathfrak{z}_n = 0$ and $\mathfrak{x}_n = \mathfrak{y}_n, \mathfrak{z}_n = 0$ on C_2; $\mathfrak{y}_n = 0$, $\mathfrak{z}_n = \mathfrak{x}_n$ on C_1; then we have

$$D(\mathfrak{x}_n) = D(\mathfrak{y}_n) + D(\mathfrak{z}_n) + 2\int_{C_1} \mathfrak{x}_n \frac{\partial}{\partial r}\mathfrak{y}_n \, ds,$$

where r is the radius, s the arc length on C_1. If $\mathfrak{x}_n$ were not equicontinuous on C_1, the lemma proved above shows easily that the last integral in this formula tends to zero as n increases. Since the vector $\mathfrak{y}_n$, if continued identically zero inside C_1, is continuous on and inside C_2, mapping C_2 on Γ_2, we have $D(\mathfrak{y}_n) \geq d_2$, and similarly $D(\mathfrak{z}_n) \geq d_1$. Hence for $n \longrightarrow \infty$ the last equality yields $d \geq d_1 + d_2$ in contradiction to the assumption $d < d_1 + d_2$. Therefore the equicontinuity of the vectors $\mathfrak{x}_n$ is established. Essentially the same reasoning remains valid for $k > 2$.

Exactly as in the case $k = 1$ it follows that we can choose a subsequence $\mathfrak{x}_n$ uniformly converging to a solution $\mathfrak{x}$ of Problem I with $D(\mathfrak{x}) = d$.[5]

Generalizations for the case of free boundaries or minimal surfaces of a different topological type (e.g., genus different from zero) follow the same lines. In the latter case the required topological structure can be established by suitable coördination of boundaries, and certain inequalities occur in a natural way as sufficient conditions.[6]

3. *The Solution Furnishes a One-to-One Mapping of the Boundaries.*[7]—That $\mathfrak{x}$ gives not only a continuous but a one-to-one mapping of the boundaries can be seen as follows (we restrict ourselves to the typical case $k = 1$): If a whole arc b on C would correspond to the same point, e.g., $\mathfrak{x} = 0$ on Γ_1, no other point of C being mapped on $\mathfrak{x} = 0$, then we could map G

conformally on the unit circle G' with a cut c along one radius OB, in such a way that b corresponds to the two edges of the cut c. This transformation transforms $\mathfrak{x}$ into $\mathfrak{x}'$ in G', so that $d = D(\mathfrak{x}) = D_{G'}(\mathfrak{x}') = D(\mathfrak{x}')$. But $\mathfrak{x}'$ is also continuous in the unit circle G, irrespective of the cut c_1 and maps the boundary of the unit circle on Γ, so that the point B and only B on the boundary C corresponds to $\mathfrak{x} = 0$. Now $\mathfrak{x}'$ cannot be a regular potential function in G, because then it must vanish on the whole diameter AOB, which contradicts our assumptions. But then the regular potential vector $\mathfrak{z}$, having the same boundary values as $\mathfrak{x}'$ would give a smaller Dirichlet integral than d, which contradicts the minimum character of d. Therefore no such arc b can occur. A similar proof holds for arbitrary k.

4. *The Solutions Are Minimal Surfaces.*—$\varphi(w) = 2\mathfrak{x}_u\mathfrak{x}_v + i(\mathfrak{x}_u^1 - \mathfrak{x}_v^2)$ is in G a regular analytic function of the complex variable $w = u + iv$. We have to show[8] that identically $\varphi(w) = 0$ holds. In the case $k = 1$ we establish this fact by using polar coördinates r, ϑ concentric to C. We substitute in the Dirichlet integral instead of $\mathfrak{x}$ another vector $\mathfrak{z}$ defined by $\mathfrak{z}(r,\vartheta) = \mathfrak{x}(r,\varphi)$, where $\varphi = \vartheta + \epsilon\lambda(r,\vartheta)$; here λ is arbitrary but sufficiently differentiable, ϵ a small parameter. By introducing r, φ as new coördinates we easily find the variational condition

$$\frac{\partial}{\partial\epsilon} D(\mathfrak{z})/_{\epsilon=0} = \int_0^1 \int_0^{2\pi} \left\{ \lambda_\vartheta \left(\mathfrak{x}_r^2 - \frac{1}{r^2}\mathfrak{x}_\vartheta^2 \right) + 2\lambda_r \mathfrak{x}_r \mathfrak{x}_\vartheta \right\} r\,dr\,d\vartheta = 0$$

which leads immediately to the boundary condition

$$\lim_{r\to 1} \int \lambda(r,\vartheta) r \mathfrak{x}_r \mathfrak{x}_\vartheta d\vartheta = 0.$$

Now $2r\mathfrak{x}_r\mathfrak{x}_\vartheta$ is a real part of the analytic function $w^2\varphi(w)$, hence a potential function. But since the value of such a potential function in any interior point of G are linear combinations of its values on a concentric circle with the radius r, containing this point, our equality expresses that this real part vanishes identically in G. Therefore we have $w^2\varphi(w) = ic$, where c is constant. But since $\varphi(w)$ is regular at $w = 0$, we have $c = 0$, hence $\varphi(w) = 0$, q.e.d.

The same argument yields for $k = 2$, if G is an annular ring, $w^2\varphi(w) = ic$. The conclusion $c = 0$ now follows easily by the variational condition with respect to the ratio of the radii.

In a way capable of generalization to arbitrary k, we can express the totality of variational conditions in the following way: $\varphi(w) = \psi''(w)$ where ψ is regular and uniform in G and where the second normal derivative of the real part of ψ vanishes on all circular boundaries.

Instead of concluding from this, that ψ is linear, one can give the following quite general proof that $\varphi = 0$. Using essentially a simple theorem on conformal mapping we can prove that $\mathfrak{x}$ solves also the follow-

ing Problem III: $D(\mathfrak{z}) = \min$, where $\mathfrak{z}$ satisfies the same conditions as $\mathfrak{x}$ in Problem I except that $\mathfrak{z}$ is allowed to be discontinuous on a prescribed cut c in G, in such a way, that $\mathfrak{z}$ maps the two edges of c continuously on the same curve in the $\mathfrak{x}$-space. Now we take as such a cut an arbitrary straight segment $v = \text{const.}$ in G and replace the minimum vector $\mathfrak{x}$ by $\mathfrak{z}(u,v) = \mathfrak{x}(u + \epsilon\lambda(u,v),v)$, where λ is zero except in a domain adjacent to one edge of c; λ may be supposed as having continuous derivatives up to the second order. The equality $\frac{\partial}{\partial\epsilon} D(\mathfrak{z})/_{\epsilon=0} = 0$ yields immediately

$$\int_c \lambda \mathfrak{x}_u \mathfrak{x}_v \, du = 0$$

and since λ is arbitrary $\mathfrak{x}_u\mathfrak{x}_v = 0$ on c; hence $\mathfrak{x}_u\mathfrak{x}_v = 0$ everywhere in G. If we take c as a segment of a straight line $u - v$ const. we obtain in the same way $(\mathfrak{x}_u - \mathfrak{x}_v)(\mathfrak{x}_u + \mathfrak{x}_v) = 0$ or $\mathfrak{x}_u^2 - \mathfrak{x}_v^2 = 0$. Hence the character as a minimal surface is established for all our solutions.

[1] For reference to literature see the report by T. Radó, "On the Problem of Plateau," *Ergebnisse Math.*, Bd. 2, 2, Springer Berlin (1933) and J. Douglas, "The Problem of Plateau," *Bull. Amer. Math. Soc.*, April (1933).

[2] Douglas' method which had been outlined in several abstracts and lectures since 1929 attains a somewhat greater generality particularly with respect to the conditions for the boundary.

[3] A detailed proof will be published in the *Ann. Math.*

[4] E.g., Hurwitz-Courant, *Funktionentheorie*, 3rd ed. Abschnitt 3, Kap. VI, § 4. Radó already has noticed the connection between this older theory and certain steps in Douglas' proof.

[5] The corresponding sufficient conditions then can be expressed in the form: $d < d_m + d_m'$ where d_m is the lower limit belonging to γ_m and d_m' that belonging to the $k - 1$ curves $\gamma_1, \ldots \gamma_k$ except γ_m, m ranging from 1 to k.

(Addition in the proof.) After this paper had been sent to the press my attention was called to a note by J. Douglas published a few weeks before in the *Journal of Mathematics and Physics* in which equivalent results for k contours and arbitrary genus on the basis of quite different methods are announced. This earlier publication establishes Douglas' priority.

[6] These conditions express that surfaces of a lower topological type (smaller genus) or surfaces consisting of separate parts furnish a larger lower limit of the Dirichlet Integral.

[7] This statement is only an illumination, not an indispensable step of the existence proof.

[8] Already T. Radó has pointed out (l. c., p. 86) that a procedure more in line with the classical calculus of variations leads to a simplification of the original proof.

ON THE THEORY OF CONFORMAL MAPPING

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In a previous note "On the Problem of Plateau"[1] a theorem from the theory of conformal mapping was mentioned in § 4. The present note gives an explicit formulation of this fact and of a more general theorem which is interesting in itself. Furthermore connections with the problems of Plateau and Douglas are discussed.

LEMMA: *A domain G in the plane of the complex variable $w = u + iv$ may be cut along an arc c of a Jordan curve; between the two edges of the cut c a one-to-one continuous correspondence, topologically equivalent to the identity, may be established. Then there exists a conformal mapping of the domain $G' = G - c$ on another domain $B' = B - b$, b being the image of c, so that corresponding points of the two edges of c are mapped in coincident points on b.*

For the applications it is sufficient to suppose c and the prescribed correspondence as piecewise analytic. Then our domain G with the correspondence of the edges of the cut c represents a Riemann manifold and can therefore, according to the elementary theory of conformal mapping,[2] be conformally transformed into a domain B of the desired form.

The lemma can be immediately generalized to the case when instead of a single cut the domain G is dissected by a finite system of cuts. With more generality we formulate the following theorem:

An abstract piecewise Riemannian manifold G in the plane of the variable $w = u + iv$ may be given as the sum of a finite (or even denumerably infinite) set of domains $G_1, G_2, \ldots$ with boundaries consisting of Jordan arcs, some of which are coördinated in a continuous one-to-one way. Then G can be mapped continuously and piecewise conformally on a domain B of the plane, so that the mapping is conformal in every domain G_ν, and still continuous on its boundaries, whereby corresponding boundary points have the same image.

Also this generalization of our lemma is a consequence of Riemann's mapping theorem, if the coördinated boundary arcs and the correspondences are piecewise analytic. But it may be pointed out that our general mapping theorem can be obtained as simply as the classical mapping theorems by solving a variation problem of the Riemann-Dirichlet type which defines the mapping function. The variation problem which for this purpose has been used[3] need only be modified by the additional condition that the admissible functions must have equal values in corresponding points.

Our statements apply also to the case when the domain G is not of genus

0 ("schlichtartig"); the case of a higher genus or of one-sided domains can be realized by a domain in the w-plane by suitable coördinations of parts of the boundaries of the domain G.

In § 4 of the previous note it was stated that our lemma provides a simple way of completing the existence proof for the problem of Plateau and the general problem of Douglas. For this purpose it was sufficient to show that with the previous denotations the solution $\mathfrak{x}$ of Problem I also solves Problem III. Otherwise a vector $\mathfrak{z}$ admissible in III and establishing a one-to-one correspondence of the edges of the cut c would yield a Dirichlet integral $d' < d$. By a conformal mapping according to our lemma, the domain $G - c$ and the vector $\mathfrak{z}$ could be transformed into a domain $B - b$ and a vector $\mathfrak{z}$ which is continuous in B and has the same Dirichlet integral, $d' < d$. Since B is conformally equivalent to a circular domain G^* there would be a contradiction between the assumption $d' < d$ and the minimum property of d.

Here a remark may be added, showing that this solution $\mathfrak{x}$ of the Plateau Problem furnishes at the same time the least possible area, compared to other surfaces of the same topological type and spanned in the curves. It may be sufficient to consider the simplest case $k = 1$ and the genus 0, further to assume Γ as a polygon. P may be a fixed polyhedron bounded by Γ and consisting of the triangles B_ν. We subdivide the unit circle G in a topologically corresponding way by triangles G_ν with piecewise analytical, e.g., circular, boundaries. The boundaries of these triangles may be called C_ν, the boundaries of the triangles B_ν may be called Γ_ν. If then we replace the Problem I, or rather a problem of the type III with the C_ν as permitted lines of discontinuity for the vectors $\mathfrak{x}$, by a new Problem IV, imposing to the vector $\mathfrak{x}$ the additional condition that $\mathfrak{x}$ maps the boundary C_ν on the boundary Γ_ν, then for the minimum d^* of the Problem IV we certainly have $d \leq d^*$. But d^* is the sum of the minima belonging to the single domains G_ν, and these minima are obviously the areas of the triangles B_ν. Therefore, d^* is the area of P, and since P may be any polyhedron, bounded by Γ, and since d is the area of the surface S, the minimum area property of S is established.

Douglas has proved this property by referring to the conformal mapping of a polyhedron on a domain in the plane. Inasmuch as the possibility of such a mapping is contained in the mapping theorem given above it appears that the present reasoning has a close relationship to that of Douglas. However, since our lemma is essentially equivalent to Riemann's mapping theorem, and since the latter is proved together with the solvability of Plateau's Problem (this was one of Douglas' original remarks) the present argument can serve to satisfy Douglas' requirement of avoiding any use of conformal mapping based on methods outside of the theory of Plateau's problem.

[1] See these PROCEEDINGS, **22**, 367–372 (1936).

[2] See, e.g., Hurwitz-Courant, *Funktionentheorie*, Berlin, 1931, Part 3, and Weyl, *Die Idee der Riemannschen Fläche*, Leipzig (1913).

[3] See, e.g., Hurwitz-Courant, *Funktionentheorie*, Part 3, and Courant, *Crelle's Jour.*, **165**, 247 (1931).

REGULAR SUBGROUPS OF A TRANSITIVE SUBSTITUTION GROUP

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It was incidentally stated in these PROCEEDINGS, **21**, 469–472 (1935), that every transitive substitution group of degree p^m, p being a prime number, contains a regular group of order p^m. In the review of this article in the *Jahrbuch über die Fortschritte der Mathematik*, **61**, 94 (1935), it was correctly stated that exceptions to this theorem appear for every value of p. In what follows we aim to establish some theorems relating to conditions under which the given theorem is true, as well as conditions under which it necessarily fails. In the article to which we referred it was noted that every transitive group of degree p^m contains a transitive Sylow subgroup whose order is a power of p and this result will be assumed in what follows. Hence it will be necessary to consider only transitive groups of degree p^m, and when the order of such a non-regular group is a power of p it obviously contains an intransitive invariant subgroup of index p whose transitive constituents are of degree p^{m-1}, since it involves p systems of imprimitivity.

We shall first prove that every transitive group of degree p^2 contains a regular group. In view of the theorem noted above we may confine our attention in the proof of this theorem to the case when the order of such a group G is p^m. It is known that G contains an invariant substitution of order p as well as a subgroup of index p whose transitive constituents are generated by the cycles of this substitution. Hence this subgoup of index p contains only one subgroup of order p which is invariant under G. This includes the pth power of every substitution in G and is contained in every regular subgroup of G. The number of the additional substitutions in such a subgroup is $p^2 - p$ and hence G contains exactly p^{m-2} regular subgroups. That is, *every transitive substitution group of order p^m and of degree p^2 contains p^{m-2} regular subgroups*. The value of m may vary from 2 to $p + 1$ and hence the largest possible number of these subgroups is p^{p-1}. A necessary and sufficient condition that these subgroups are invariant under G is that m does not exceed 3.

It was noted above that the intransitive subgroup of index p under G composed of all its substitutions which do not interchange any of the cycles of its substitution of order p which is invariant under G contains only one invariant subgroup of order p under G. Hence it gives rise to a commutator subgroup of index p^2 under G which again contains only one invariant substitution under G. As this commutator subgroup gives rise to a commutator subgroup of index p^3 under G, etc., it results that the given intransitive subgroup contains one and only one invariant subgroup under G for each of the orders p, p^2, ..., p^{m-1}. Each of these includes all of those which precede it. The invariant subgroup of order p^2 in this set is especially interesting since it involves only substitutions of degree $p^2 - p$ besides the p invariant substitutions under G.

Having established the existence of an infinite system of transitive groups of a degree which is of the form p^m, $m > 1$, such that each of them contains at least one regular subgroup, we proceed to consider infinite systems of transitive groups whose degrees are of this form but which do not involve any regular group as a subgroup. We shall first consider such a system of degree p^3. To construct this system we establish a p^p isomorphism between p transitive groups of degree p^2 and of order p^3 in such a way that the co-sets composed of substitutions of degree $p^2 - p$ correspond, where the symbol p^p is employed instead of the more common but longer symbol (p,p,p, ..., p times). If we extend the intransitive group thus formed by means of the product of the substitution of order p which merely interchanges the corresponding letters of the transitive constituents in the intransitive group and a substitution of degree $p^2 - p$ from one of these constituents there results a group in which all of the additional substitutions are non-regular and hence this G contains no regular group as a subgroup. This G exists for every value of the prime number p. In the special case when $p = 2$ such a group is of degree 8 and of order 32. It is given as number 14 in volume 1 (1935) of my *Collected Works*, page 389.

The groups of this system can clearly be employed in a similar manner to construct an infinite system of groups of degree p^4 such that no group of the system contains a regular subgroup. As this process can be continued indefinitely there results the following theorem: *There exists a transitive group of degree p^m,$m > 2$ for every prime number p, such that it does not contain a regular group as a subgroup but every transitive group of degree p^2 contains such a subgroup.*

Suppose that G is a transitive group of degree p^m and that the transitive constituents of its intransitive subgroup of index p are regular. The subgroup of G composed of all its substitutions which omit a given letter is of degree $p^m - p^{m-1}$ since the number of letters omitted by this subgroup is a divisor of the degree and a multiple of p^{m-1}. As the construction of G comes under the general theory of constructing all the regular groups of

order p^m it results that G involves a regular subgroup. That is, *every transitive group of degree p^m which involves an intransitive subgroup of index p whose transitive constituents are regular involves a regular subgroup.* A simple illustration of this theorem is the group of order 8 and of degree 4. When the transitive group is of order p^{m+1} the substitutions which are of degree less than p^m are in the central of the intransitive subgroup of index p. When the order of a transitive group of degree p^m has a maximal value it contains a regular subgroup since it is completely determined by its order, and every group of degree p^m whose order is a power of p is found in a Sylow group of the symmetric group of degree p^m.

GENERALIZED INTEGRALS AND DIFFERENTIAL EQUATIONS

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The following theorems have been proved by the author:

1. *Generalization of the Integral.*—Theorem: In the interval $X_0 \leq x \leq X_1$ consider a function $f(x)$, approximable by continuous functions and satisfying the inequality $|f(x) - f(X_0)| < F$, and n continuous functions $g_1(x), g_2(x), \ldots, g_n(x)$ of the bounded total variations $G_1, G_2, \ldots, G_n$. Suppose that two functions a and b of $f, x, g_1, g_2, \ldots, g_n$ in the domain

$$|f - f(X_0)| \leq F, X_0 \leq x \leqq X_1, |g_1 - g_1(X_0)| \leq G_1, \ldots, |g_n - g_n(X_0)| \leq G_n$$

admit of continuous partial derivatives with respect to all arguments. Then, for every sequence of continuously differentiable functions $f_k(x)$, $k = 1,2\ldots$ satisfying the inequality $|f_k(x) - f(X_0)| < F$ and tending to $f(x)$ as k tends to ∞, the limit

$$L = \lim_{k \to \infty} \int_{X_0}^{x} a\,(f_k(x), x, g_1(x), \ldots, g_n(x))\, db(f_k(x), x, g_1(x), \ldots, (g_n(x))$$

exists.

We write

$$L = \int_{X^0}^{x} a(f(x), x, g_1(x), \ldots, g_n(x))\, db(f(x), x, g_1(x), \ldots, g_n(x)).$$

Remark. This integral is *not* identical to the Stieltjes integral. For the function $f(x) = 0$, $0 \leqq x < 1$, $f(1) = 1$, we have for instance

$$\int_0^1 f(x)\, df(x) = \frac{f^2(1) - f^2(0)}{2} = \frac{1}{2}.$$

The Lesbesque-Stieltjes integral would be 1.

2. *Ordinary Differential Equations.*—Theorem 2:

Assumptions: In the interval $0 \leqslant x \leqq X$, the continuously differentiable functions $f_k(x)$, $k = 1,2,\ldots$ converge to a function $f(x)$. $f_k(0) = 0$, $k = 1,2, \ldots, \infty$. The continuously differentiable functions $g_{ik}(x) i = 1, \ldots, n$; $k = 1,2, \ldots, \infty$ tend to the continuous functions $g_i(x)$ as $k \longrightarrow \infty$. The total variations of $g_{ik}(x) - g_i(x)$ tend to zero and the total variations of $g_{ik}(x)$ are uniformly bounded by numbers $G_i > 0$, $i = 1, \ldots, n$. For some $\epsilon > 0$ the quantities $a_0, a_1, \ldots, a_n$ are functions of z, y_i, u in the domain

$$|z| \leq F, |y_i| \leq G_i, |u| < \epsilon + 2FM_0 + \sum_{l=1}^{n} (e^{2FN} - e^{FN} + M_l e^{FN})G_l$$

and are absolutely bounded by $M_1, M_2, \ldots, M_n$. The functions $a_0, \ldots, a_n$ are all continuously differentiable and the first derivatives of a_0 are bounded by $N > 0$ and satisfy a Lipschitz condition of exponent 1.

Assertion: The solution $u_k(x)$ of $u_k(0) = 0$ and

$$du_k(x) = a_0(f_k(x), g_{ik}(x), \ldots, g_{nk}(x), u_k(x))df_k(x) + \sum_{l=1}^{n} d_l(f_k(x), g_{ik}(x), u_k(x))dg_{lk}(x)$$

exists for $0 \leq x \leq X$ and all k, and tends to a limit function $u(x)$ as $k \longrightarrow \infty$. We have

$$|u(x)| \leq FM_0 + \sum_{l=1}^{n} (e^{2FN} - e^{FN} + M_l e^{FN})G_l.$$

We call $u(x)$ the solution of

$$du(x) = a_0(f(x), g_{ik}(x), u(x))\, df(x) + \sum_{l=1}^{n} a_l(f(x), g_i(x), u(x))dg_l(x) \quad (1)$$

and the initial condition $u(0) = 0$.

A similar theorem may be obtained for systems of equations of the form (1), with unknown functions $u(x), v(x), \ldots$, *one* function $f(x)$ of Baire's first class and a certain number of functions of bounded and continuous variation $g_1(x), g_2(x), \ldots$ intervening in the equations

3. *Initial Problem for Hyperbolic Systems.*—Theorem 3: Consider the following system of partial differential equations for n functions $\varphi_1, \varphi_2, \ldots, \varphi_n$ of two independent variables α and β:

$$\sum_{k=1}^{n} a_{ik} \frac{\partial \varphi_k}{\partial \alpha} = 0, i = 1, \ldots, m < n; \quad \sum_{k=1}^{n} a_{ik} \frac{\partial \varphi_k}{\partial \beta} = 0, i = m+1, \ldots, n;$$

for $n \geqslant 2$.

The initial line is a segment σ of the line $\alpha = \beta$ and on σ the values of $\varphi_1, \ldots, \varphi_n$ are given as functions of the arc length τ. Assume that (i)

for all values of τ in σ the points of a Euclidean $\varphi_1, \ldots, \varphi_n$ space with coördinates $\varphi_1(\tau), \varphi_2(\tau), \ldots, \varphi_n(\tau)$ lie within a sphere S_ρ of radius ρ; (ii) for all points of a concentric sphere $S_{2\rho}$ the determinant of the functions $a_{ik}(\varphi_1, \ldots, \varphi_n)$ satisfies the condition:

$$|a_{ik}| \neq 0;$$

(iii) throughout $S_{2\rho}$ the a_{ik} have continuous partial derivatives up to the fourth order with respect to $\varphi_1, \ldots, \varphi_n$; (iv) there exists a transformation with constant coefficients γ_{ik}, of determinant $\neq 0$, $\psi_i = \sum_{k=1}^{n} \gamma_{ik}\varphi_k$, $i = 1,2, \ldots, n$, such that on the initial line the function ψ_1 is continuous, while $\psi_2, \ldots, \psi_n$ are continuous and of bounded variation.

Then there exists for every interior point of σ an α,β-neighborhood where a continuous solution of the initial problem exists. Under "solution" we understand the (uniquely determined) limit of solutions for approximating continuously differentiable initial values $\phi_{ij}(\tau)$, $i = 1, \ldots, n$; $j \longrightarrow \infty$ subject only to the following conditions: For every j the point with components $\phi_{ij}(\tau), \phi_{2j}(\tau), \ldots, \phi_{nj}(\tau)$ for τ in σ belongs to S_ρ; moreover

$$\psi_{1j}(\tau) = \sum_{k=1}^{n} \gamma_{1k}\,\phi_{kj}(\tau) \longrightarrow \psi_1(\tau) \text{ as } j \longrightarrow \infty$$

and the functions

$$\psi_{ij}(\tau) = \sum_{k=1}^{n} \gamma_{ik}\,\phi_{kj}(\tau),\ i = 2, \ldots, n,$$

and their total variations tend to $\psi_i(\tau)$ and its total variation as $j \longrightarrow \infty$.

4. *Elliptic Equations of Monge Ampère Type.*—Theorem 4: Consider a sequence of Monge-Ampère equations

$$A_n r + B_n s + C_n t + rt - s^2 = E_n \qquad (2)$$

in which, as usual, p, q, r, s, t stand for the first and second derivatives of a function $x(u, v)$ and where A_n, B_n, C_n, E_n are analytic functions of the arguments u, v, x, p, q as long as these belong to a fixed bounded domain D of a complex u, v, x, p, q, space, and where $A_n, \ldots, E_n$ are real for real u, v, x, p, q of D and such that there

$$\Delta_n = 4(A_nC_n + E_n) - B_n^2 > 0 \qquad (3)$$

while for the whole of D

$$|\Delta_n| > 0.$$

Suppose that in D

$$A_n, B_n, C_n, E_n \rightrightarrows A, B, C, E(u, v, x, p, q) \text{ as } n \longrightarrow \infty,$$

and

$$|\Delta| = |4(AC + E) - B^2| > 0.$$

Suppose furthermore that for every n and a circle K: $(u - u_0)^2 + (v - v_0)^2 < \epsilon$ of the real u,v-plane we know a real analytic solution $x_n(u,v)$ of (2) which together with its first derivatives $p_n(u,v)$ and $q_n(u,v)$ tends uniformly to a function $x(u,v)$ and its derivatives $p(u,v)$ and $q(u,v)$, such that for every n and u,v in K $(u, v, x_n(u,v), p_n(u,v), q_n(u,v))$ lies in D and the same is true for $(u, v, x(u,v), p(u,v), q(u,v))$.

Then, for (u,v) in K, there exist two parameters ζ and η such that $u, v, x(u,v), p(u,v), q(u,v)$ are analytic functions of ζ and η in $\zeta^2 + \eta^2 < 1$. The map $\zeta, \eta \longrightarrow u, v$ is one to one; x has second derivatives r, s, t and satisfies throughout K

$$Ar + Bs + Ct + rt - s^2 = E, \tag{4}$$

except possibly at points satisfying the analytic equation

$$\frac{\partial(u,v)}{\partial(\zeta,\eta)} = 0.$$

The proof is an application of the Theorem 3 of the foregoing section to the analytic continuation of the functions $x(u,v)$ into a complex domain, similar to the one the author used in former papers. This application is rendered possible by the remark, that from (3) one can deduce[1] $r_n + C_n \neq$ throughout K; hence there exists a constant k such that for all n the function $x_n(u,v) + ku^2$ is monotone on every line $v = \text{const.}$, so that, for a suitable subsequence of n, the functions $u, v, x_n(u,v) + ku^2, p_n(u,v) + 2ku$ tend *together with their variations* to $u, v, x(u,v) + ku^2, p(u,v) + 2ku$, while the functions $q_n(u,v)$ tend uniformly to $q(u,v)$. This last remark may be utilized in order to omit in the Theorem the assumption of the convergence of $p_n(u,v)$ and $q_n(u,v)$ to $p(u,v)$ and $q(u,v)$ **provided** $p(u,v)$ **and** $q(u,v)$ **are continuous,** as it can be shown that the uniform convergence of a subsequence of $p_n(u,v)$ and $q_n(u,v)$ follows for every concentric circle in K. On the other hand, after a suitable contact transformation which, as is well known, preserves the Monge-Ampère type and the elliptic character (3), even the assumption of the continuity of $p(u,v)$ and $q(u,v)$ may be obtained as consequences of the convergence of the $x_n(u,v)$. Thus we have the following

Theorem 5: Suppose that, under the assumptions of Theorem 4 as to $A_n, B_n, C_n, E_n, A, B, C, E$, there exists a circle K of the real u,v-plane where for every n there exists a real and analytic solution of (2) with derivatives $p_n(u,v)$ and $q_n(u,v)$ such that for u,v in K the point $(u, v, x_n(u,v), p_n(u,v), q_n(u,v))$ lies in D. Then there exists a subsequence of $x_n(u,v)$ which in concentric circle K' tends to a function $x(u,v)$ and two parameters ζ, η such

that u, v, x are analytic functions of ζ, η, the map of $\zeta^2 + \eta^2 < 1$ on K' is one to one, and $x(u,v)$ satisfies (4) except possibly at points where $\frac{\partial(u,v)}{\partial(\zeta,\eta)} = 0$.

Theorem 5 is of great importance for the *treatment* of equation (4) *in the large*, as it is necessitated by several problems of the differential geometry in the large, especially in connection with a Lemma[2] that under certain conditions permits to rule out the possibility $\frac{\partial(u,v)}{\partial(\zeta,\eta)} = 0$. We intend to take up those applications at another place.

[1] Cf. F. Rellich, "Zur ersten Randwertaufgabe bei Monge-Ampèreschen Differentialgleichungen vom elliptischen Typus," *Math. Ann.*, **107**, 505–513 (1932). Hans Lewy, "A Priori Limitations for Solutions of Monge-Ampère Equations," *Trans. Am. Math. Soc.*, **37**, 417–434 (1935).

[2] Hans Lewy, "On the Non-Vanishing of the Jacobian of Certain Mappings," *Bull. Am. Math. Soc.* (in press at present).

ON THE CONNECTIVITY RING OF A BICOMPACT SPACE
(*Second Note*)

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1. If we map a bicompact space B in a one-one continuous manner on a closed subset of a cartesian space C of suitable finite or transfinite dimensionality, the cycles of the open space $C - B$ complementary to B will determine a topological invariant, called the *connectivity ring* of B, which will be independent of the mapping of B on C.[1] In this note, we shall indicate, very briefly, how the connectivity ring of an arbitrary space B can be defined directly in terms of the internal structure of B. If the space B is bicompact, and if it is represented as a subspace of a cartesian space C, it will be possible to identify the connectivity ring of B, as here defined, with the connectivity ring determined by the cycles of $C - B$. (The theorem establishing this identification will be the *duality theorem* in all its generality.)

2. By a *closed domain* of B will be meant the closure of any open set of B. Every closed domain α of B will obviously be associated with a well determined closed domain β, such that each of the domains α and β is the closure of the complement of the other. Moreover, the two domains α and β will intersect in a nowhere dense, closed set α' which will be called the *shell* of α and β.

The point set α' may be the null set, since the domains α and β may be open, as well as closed; it may be the shell of more than one pair of associated domains α and β (cf., for example, the case where B is a plane and α' a Brouwer set forming the common frontier of three or more plane regions).

3. The closed domains of B determine an abstract *non-commutative* ring R obtained in the following manner. From every pair of associated closed domains α_i and β_i we arbitrarily pick one of the domains, say α_i, and assign to it a mark a_i, while to the other domain β_i we assign the mark $b_i = 1 - a_i$. Morever, to the shell α_i' of α_i and β_i we assign the mark a_i'. (If α_i' is the shell of more than one pair of associated closed domains there will be more than one mark assigned to it.) Finally, to the entire space B we assign the mark 1 and to the null set the mark 0. The ring R will be the ring of all finite polynomials in the a_i's and the a_i''s, with integer coefficients λ after suitable identifications have been made among the polynomials of the ring. (By a slight generalization we could have allowed the coefficients λ themselves to be the elements of an arbitrary ring.)

We now make the necessary identifications. (*a*) Two marks with different subscripts i and j will be made to commute, unless both of them are primed, in which case they will be made to anti-commute.

$$\begin{aligned} a_i a_j &= a_j a_i \\ a_i a_j' &= a_j' a_i \ (i \neq j) \\ a_i' a_j' &= -a_j' a_i' \end{aligned} \tag{1}$$

(*b*) Two marks with the same subscript i will be made to condense according to the following rules:

$$\begin{aligned} a_i a_i &= a_i \\ a_i a_i' &= a_i' \\ a_i' a_i &= 0 \\ a_i' a_i' &= 0 \end{aligned} \tag{2}$$

Relations (1) and (2) will obviously enable us to reduce every polynomial of R to a sum of terms of the form

$$\lambda a_{i_1}' a_{i_2}' \ldots a_{i_m}' a_{j_1} a_{j_2} \ldots a_{j_s} \quad (\lambda \text{ an integer}), \tag{3}$$

where the primed marks all precede the unprimed ones and where the subscripts $i_1, \ldots, i_m, j_1, \ldots, j_s$ are all distinct.

In addition to (*a*) and (*b*), which are general in character, there will be a third set of identifications depending essentially on the topological structure of B. It can easily be shown that every polynomial π made up of sums of the forms (3) can be expressed in a unique manner as a sum of terms of the form

$$a_{i_1}' a_{i_2}' \ldots a_{i_m}' a_{j_1} a_{j_2} \ldots a_{j_s} b_{k_1} b_{k_2} \ldots b_{k_t}, \ (b_k = 1 - a_k), \tag{4}$$

where the subscripts appearing in (4) also appear in the polynomial π and where every subscript appearing in π appears exactly once in each term (4). We shall equate to 0 every product (4) such that the intersection of the closed sets associated with the factors of (4) is the null set; that is to say, such that

$$\alpha'_{i_1}\alpha'_{i_2}\ldots\alpha'_{i_m}\alpha_{j_1}\alpha_{j_2}\ldots\alpha_{j_s}\beta_{k_1}\beta_{k_2}\ldots\beta_{k_t} = 0$$

4. An *elementary m-chain* E of B will be a monomial of the form

$$E = a'_{i_1}a'_{i_2}\ldots a'_{i_m}a_{j_1}a_{j_2}\ldots a_{j_s} \text{ (subscripts all distinct)} \qquad (5)$$

of degree m in the primed variables but of arbitrary degree in the unprimed variables. An *m-chain* K of B will be an arbitrary finite linear combination of elementary m-chains

$$K = \sum\lambda_i E_i \qquad (\lambda_i \text{ integers}). \qquad (6)$$

A general element of the ring R may be regarded as a sum of m-chains, not necessarily of the same dimensionality. An m-chain K and an n-chain L will be said to be in *general position* with respect to one another if the same subscript never appears in both of them. If an m-chain K and an n-chain L are in general position, we shall have, at once,

$$KL = (-1)^{mn}\,LK, \qquad (7)$$

by (1).

The *derivative* of an elementary m-chain (5) will be the $(m+1)$-chain

$$E' = \sum_{k=1}^{s} a'_{i_1}a'_{i_2}\ldots a'_{i_m}a_{j_1}\ldots a_{j_{k-1}}a'_{j_k}a_{j_{k+1}}\ldots a_{j_s} \qquad (8)$$

formed by adding all terms that can be obtained from (5) by changing a single unprimed mark a_{j_k} into the corresponding primed mark a'_{j_k}. If E contains no unprimed marks, its derivative vanishes. The derivative of a_i is obviously a'_i, the derivative of 1 is 0. *In forming the derivative of E it is essential that E be in the form* (5), *with the primed variables preceding the unprimed ones.*

The *derivative* of an m-chain (6) will be the $(m+1)$-chain M' determined by the usual formula,

$$K' = \sum\lambda_i E'_i. \qquad (9)$$

Relations (1) and (2) give us, at once, the classical equations

$$K'' = (K')' = 0 \qquad (10)$$

and

$$(KL)' = K'L + (-1)^n KL', \qquad (11)$$

where n is the dimensionality of L.

As soon as we have established (10) and (11) we can complete the discussion in the customary manner. An m-chain will be *exact* if its derivative vanishes, it will be *derived* if it is the derivative of some $(m-1)$-chain. By (10), every derived chain will be exact; therefore, the group G_D^m of all derived m-chains will be a subgroup of the group G_E^m of all exact m-chains. The residue group G_E^m mod G_D^m will be the *m-th connectivity group of B*. Finally, by (11), the product of two exact chains will be exact and the product of an exact chain by a derived chain or of a derived chain by an exact chain will be derived. Therefore, the exact chains will generate a sub-ring R_E of R and the derived chains an ideal R_D of R_E. The ring R_E mod R_D will be the *connectivity ring* of the space B.

[1] Cf. a previous note under the same title communicated to these PROCEEDINGS on March 30, 1936. A more detailed account of the theory outlined in the present and previous notes is now being prepared for publication. Moreover, an alternative treatment, from quite another angle, will appear in the *Ann. Math.* for July of this year.

PHYTOPHARMACOLOGICAL REACTIONS OF NORMAL, TOXIC AND ATOXIC SERA

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Introduction.—While physiology is broadly divided by specialists into *zoo*physiology and *phyto*physiology, pharmacology as studied in most of our medical and research institutions has hitherto concerned itself almost exclusively with the effects of drugs on animals (and not plants) so that, strictly speaking, it is *zoo*pharmacology. Fifteen years ago the senior author began a systematic inquiry into the effects of drugs on living plants, as compared with their action on animals, and for convenience designated such studies as *phytopharmacology*.[1] The effects of drugs and poisons on plants may be observed in various ways. Studies may be made on germination of seeds; on the growth of roots, stems, leaves, flowers and fruits; on transpiration, respiration, photosynthesis and other metabolic functions; on protoplasmic streaming and plant movements; and on the action of yeasts, fungi, etc.[2]

A most useful method for qualitative and quantitative investigation was found to be comparison of the root growth of seedlings of *Lupinus albus*. Briefly, the procedure is as follows: Seeds of *Lupinus albus* are soaked in tap water overnight and planted the next morning in finely ground sphag-

num containing sufficient moisture. They are allowed to germinate in the dark until the single, straight and well-demarcated roots are from 30 to 45 mm. long, when they are ready for experimentation. The length of the roots is carefully measured in millimeters and the seedlings are immersed in upright, hard-glass test tubes filled with equal parts of distilled water and Shive solution, containing definite concentrations of magnesium sulphate, diacid potassium phosphate and calcium nitrate.[3] Other series of seedlings from the same crop are placed in physiological solution plus small quantities of unknown chemicals to be tested. The whole outfit is then incubated in the dark at a temperature of 12°C. for 24 hours, after which interval the length of the roots is measured again. The ratio of the growth of roots immersed in solution containing the unknown chemical to the growth of the controls is known as the phytotoxic index or index of growth (index = X/N). In this way any desired number of unknown compounds may be tested simultaneously under the same light, temperature and other conditions. Such studies revealed that living plant tissues are generally more sensitive to the action of certain chemicals than test objects derived from the animal kingdom and logically suggested a study of phytotoxic indices given by bloods from normal and pathological conditions.

Toxic Sera.—Phytopharmacological examination of several thousand normal blood sera in 1% solution gave 75% as the average phytotoxic index. On the other hand, blood sera procured from individuals in certain abnormal physiological and pathological conditions proved to be definitely toxic. Thus phytopharmacological studies established the presence in the blood serum, plasma, whole blood, saliva, tears and other secretions of menstruating women of a toxin (menotoxin) which is absent from those body fluids during the intermenstrual period.[4,5] Again, in this way it was discovered that blood sera from pernicious anemia patients contained a toxin not found in specimens from cases of ordinary secondary anemia, leukemia, cancer, tuberculosis and syphilis.[6,7] Very recently, phytopharmacological examination of a number of sera from patients with malignant aplastic anemia indicated the presence of a toxin in such cases, too. These findings proved useful in facilitating differential diagnosis of pernicious anemia and offered a criterion for evaluation of various therapeutic procedures.[8,9] Another characteristic phytotoxic reaction was discovered by Macht and Pels in connection with a study of blood sera from all kinds of dermatoses. The blood sera of the baffling disease pemphigus revealed a toxicity which differentiated it from that of other skin diseases simulating it.[10,11,12,13] Over 2000 specimens of blood thus studied have established the value of the phytopharmacological test in diagnosing pemphigus from various pathological conditions.

Blood sera from leprosy patients were also found to give a very toxic index of growth, a circumstance which strikingly distinguishes this disease

from tuberculosis and syphilis.[14,15,16] Finally, sera from 100 cases of trachoma indicated that the blood of that disease also exerts a very toxic effect on the growth of Lupinus seedlings.[17,18]

Table 1 shows the toxicity of sera from normal individuals and from patients with the various diseases mentioned above. Table 2 gives the phytotoxic indices of specimens from diseases the sera of which yield a reading that does not substantially deviate from that of normal human blood. It is interesting to note that blood sera from eclampsia are not toxic, a finding which seems to agree with the newer view regarding that dangerous complication of pregnancy, as opposed to the older toxemic theory.[19]

TABLE 1

TOXIC SERA

KIND OF BLOOD SERUM	AV. NO OF CASES	PHYTOTOXIC INDEX
Normal human	500	75%
Menstrual	50	51%
Pernicious anemia	50	44%
Aplastic anemia	10	56%
Pemphigus	200	59%
Leprosy	22	47%
Trachoma	100	48%
Hodgkin's disease	10	60%

TABLE 2

NON-TOXIC SERA

KIND OF BLOOD SERUM	PHYTOTOXIC INDEX
Syphilis	81%
Tuberculosis	78%
Scarlet fever	79%
Measles	80%
German measles	80%
Varicella	80%
Eclampsia	75%
Post-puerperal (12 weeks)	80%

Comparison of Normal Blood Sera of Different Animals.—In the present paper the authors wish to announce new phytopharmacological data, derived from studies of the normal blood sera of various animals and in certain hitherto unexamined pathological conditions. Normal blood sera from a large number of different animals revealed that their toxicity for *Lupinus albus* seedlings was practically identical with that of normal human sera. Phytotoxic indices of from 70 to 75% were given by sera from the horse, ox, sheep, dog, cat, hog, rabbit, opossum, woodchuck, guinea pigs, rats and mice; from the hen, duck, goose, turkey and pigeon; from frogs and toads; and from the stingaree, goldfish, catfish, chub and carp. Reptilian blood was a striking exception. Sera from different species of turtle, from the iguana, chuckawalla and gila monster gave very toxic readings. Curiously enough, the alligator's blood was found to be non-toxic. On the other hand, blood sera from various non-poisonous as well as from poisonous reptiles, i.e., from the black snake, garter snake, bull snake, water snake, rattlesnake, copperhead, moccasin and cobra—all markedly inhibited plant growth. It is interesting to note that the blood of the domestic hen yielded a lower phytotoxic index than that obtained with the serum of any other warm-blooded animal studied.

Atoxic Sera.—During the past year the present authors have been engaged in a study of blood sera from a series of virus diseases, which

yielded some interesting data on these etiological agents as a class. Such blood specimens were obtained from cases of experimental vaccinia in the rabbit and rat, fowl pox in the chicken, herpes simplex in the rat, virus fixé (rabies) in the rabbit and guinea pig, virus III in the rabbit, X-virus in the cat, Rous's sarcoma in the chicken, Shope's fibroma in the rabbit, infectious myxomatosis in the rabbit, Rivers' lymphocytic chorio meningitis in the guinea pig, etc.

The blood sera of all these virus diseases, examined by Macht's phytopharmacological method on *Lupinus* seedlings, yielded indices much higher than those given by specimens from normal animals of the same species and may be designated as *atoxic*. The atoxicity of these sera, of course, is of as much interest as the toxicity of the sera from pernicious anemia, pemphi-

TABLE 3

SERA FROM VIRUS DISEASES

KIND OF BLOOD SERUM	ANIMAL INOCULATED	PHYTOTOXIC INDEX OF CONTROL	PHYTOTOXIC INDEX OF VIRUS SERUM
Fowl pox	chicken	71%	80%
Vaccinia	rabbit	73%	80%
Vaccinia	rat	67%	78%
Herpes simplex	rabbit	72%	84%
Virus fixé	rabbit	75%	61%
Virus fixé	guinea pig	81%	65%
Virus III	rabbit	72%	84%
X-virus	cat	70%	65%
Rous's tumor	chicken	66%	92%
Shope's fibroma	rabbit	77%	96%
Infectious myxomatosis	rabbit	75%	85%
Rivers' lymphocytic chorio meningitis	guinea pig	79%	102%
Poliomyelitis	monkey	61%	62%
Tetanus toxin alone, 86%	rabbit	75%	63%
Strychnine nitrate, 93%	rabbit	77%	61%

gus, leprosy and the other diseases already enumerated. The high readings are of interest also when considered together with similar findings made by Macht and Pels in their studies on blood sera from cases of varicella, measles, German measles and scarlet fever. The chief exception apparently was virus fixé. The toxicity of this blood, however, is probably due to the convulsions rather than to the specific virus of rabies because similar findings were obtained in case of tetanus and strychnine poisoning. Virus fixé alone, or when added to normal blood serum *in vitro*, did not produce a toxic effect.[20] Similarly, pure tetanus toxin, mixed with normal blood in the test tube, and strychnine solutions, added to normal sera in test tubes, produced but little increase in the toxicity, while blood obtained from animals during tetanus or strychnine convulsions was found to be very toxic. The powerful clonic and tonic convulsions of the skeletal

muscles evidently set free poisonous decomposition substances producing a toxic effect on plants.

Table 3 shows the phytopharmacological readings obtained with sera from different virus diseases and with tetanus and strychnine poisoning. Curiously enough, a series of blood specimens from monkeys infected with poliomyelitis did not give readings comparable to those of other virus diseases. Sera from animals thus infected yielded phytotoxic indices within the normal range. The findings are of special interest when compared with the data obtained concerning blood sera from ordinary bacterial and protozoan infections. All the latter gave normal readings. It is well to note that both tuberculosis and syphilis also give phytotoxic indices slightly higher than those of normal sera. The toxicity of trachoma blood, already mentioned, leaves the etiology of that disease still *sub judice*. There are those who regard it as a bacterial infection; others who deem it a virus disease; and still others who consider it a systemic disease complicated by local infection of the eyes. The phytopharmacological examination of sera from 100 trachoma cases leaves that disease still in the doubtful class.

Summary.—(1) Solutions of normal human blood in plant-physiological media produce a definite inhibition of root growth of *Lupinus albus* seedlings, which yield an average phytotoxic index of 75%.

(2) Normal blood sera from a large variety of different animals give phytotoxic indices practically identical with that of normal blood. The principal exception was the blood of reptiles. Blood sera from non-venomous, as well as those of venomous snakes, were all toxic for plant protoplasm.

(3) A marked toxicity for *Lupinus* seedlings is exhibited by sera from certain diseases, i.e., from pernicious anemia, pemphigus and leprosy.

(4) Blood specimens from a series of virus diseases yielded atoxic readings, that is, were less toxic for plant growth than normal blood sera.

(5) Blood sera from monkeys infected with poliomyelitis give readings within the normal range, while that obtained from trachoma patients exerts a marked toxicity.

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CHANGING DIRECT CURRENT TO ALTERNATING CURRENT BY MEANS OF THYRATRONS

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Read before the Academy, April 27, 1936

The use of direct current rather than alternating for transmission of electric power has many well recognized advantages, but has been considered impracticable for lack of a satisfactory method of changing the high voltage direct current into alternating current at the end of the line, for distribution to customers.

Seven years ago there was reported in this journal a method of controlling an arc discharge by means of a grid.[1] One of the most interesting applications of such grid-controlled arc devices, or *Thyratrons*, is that of "inverting" direct current into alternating. We have devoted much study to this problem, a brief summary of which is here presented.

The Constant-Current Circuit.—A number of inverter circuits have been investigated. They include (1) the simple phase-commutated parallel type inverter,[2] (2) the series type inverter[3] and (3) the harmonic-commutated inverter.[4] All of these have given excellent operation in the laboratory; but when the data obtained in the small scale laboratory tests have been extrapolated to higher power, new phenomena have been encountered, indicating the need for further research. We have been able to carry out such research, without the wastefulness usually attendant upon large-scale experiments, by using a *constant-current* circuit,[5] in which short-circuit failures do no harm. Complete tests were first made at low power (10 amps., 250 volts) on the bench; then at full voltage and small current (10 amps., 15,000 volts) in a carefully protected room in the laboratory; and finally at full power, viz., 200 amps., 15,000 volts, with engineering equipment kindly loaned to us by Dr. Alexanderson.

The constant-current circuit is shown in figure 1. Beginning at the top, constant-voltage 3-phase alternating current from the power mains is

first changed to *constant current* by a so-called "monocyclic network" of capacitors and reactors. We have given much study to the characteristics of this monocyclic network, and have found that high voltage transients are absent under all conditions if, and only if, the capacitative and inductive impedances are equal. This applies even to conditions of failure and short-circuit, providing the reactances do not change their value, by saturation, during failure.

The constant current is then transformed to the desired voltage and rectified in a conventional circuit of the type used in modern radio broadcasting, but with this important difference: that if a tube fails to rectify, the "arc-back" current is limited to the normal constant current of the line; and is usually limited in duration to one half-cycle, since the voltage drops to nearly zero and allows the arc to go out.

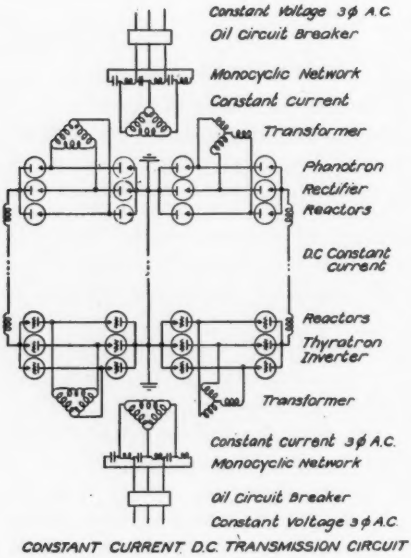

FIGURE 1

Constant-current rectifier and inverter circuit.

These circuit elements thus furnish *constant current d-c* to the middle portion of the circuit. This portion may be of any length, but in our tests it was only a few feet, since its purpose was to serve as a source of direct current to be changed into alternating.

The Inverter.—It will be noted that the circuit (Fig. 1) is symmetrical about this middle portion; the lower half, which changes (inverts) the direct current back into alternating current, is an exact image of the upper half, except for the grids in the tubes of the lower half, and apparatus, not shown, for exciting these grids. This emphasizes the fundamental similarity between *rectifier* and *inverter*. The inverter is, as its name signifies, an *inverse rectifier*—a rectifier run backward.

The problem of inversion, however, is much more difficult than that of rectification, and calls for a detailed study under operating conditions. Thyratrons are much more circuit-sensitive than either high-vacuum tubes or gaseous-discharge rectifiers: (1) An inverter Thyratron must start instantly, within a few microseconds, when called on, otherwise its *mate*

loses the opportunity to shift the load; for the current in a Thyratron tube cannot, in general, be stopped by making its grid negative, but requires that the load be removed by making its anode negative. (2) It must deionize during the available time of negative anode voltage. (3) It must not arc-back while the anode is negative. (4) The grid must prevent conduction in the forward direction during the period of high, positive anode voltage.

Each of these 4 functions is as dependent on the circuit as on the tube. For example, in the first case, the "firing" voltage applied to the grid may be wrongly or inaccurately timed, or may not be high enough, or may have insufficient power, or its rate of rise may be so slow that appreciable vari-

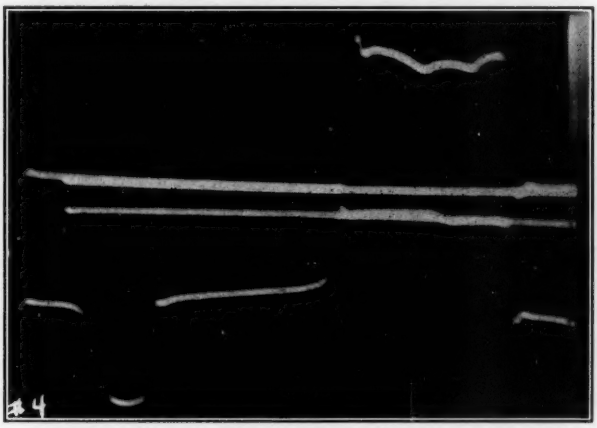

FIGURE 2

Oscillograms of grid voltage and tube current in Thyratron inverter. Lower curve, voltage applied to grid; upper curve, current in anode lead.

ations in time of firing will be caused by small changes in the voltage at which the tube starts, such as may be caused by fluctuation of ambient temperature. We have encountered all of these conditions. The problem has been solved by a special grid circuit which gives a very steep voltage wave, and which is "stiff" in the turn-on direction, and "weak" in the turn-off direction. Figure 2 shows the voltage applied to the grid by this circuit. On the other hand, tubes of certain designs have shown large variations in firing voltage, others excessive power for starting, some an appreciable time delay. It has been possible to eliminate these features in tube design as a result of these findings. Similarly, it has been necessary to avoid too large a commutating voltage, resulting in frequent arc-backs,

and too small, with insufficient time for deionization; also too large and stiff bias voltage, on the one hand, with frequent cathode-spot formation on the grid, and too small or weak bias on the other, resulting in loss of

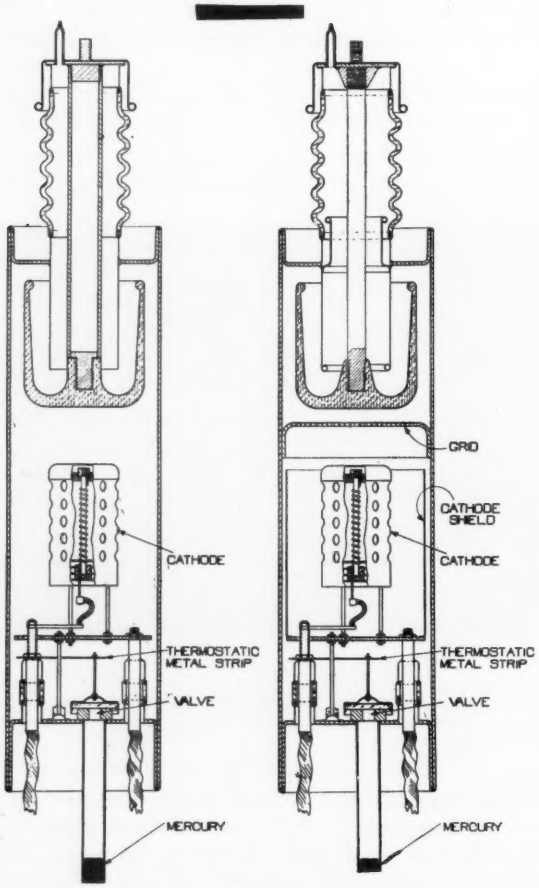

FIGURE 3

Experimental Phanotron (left) and Thyratron (right) tubes used in inverter tests.

control by the grid. These problems, too, have been made easier by study and adaptation of tube design. More detailed results of these studies will be pdblished in *Physics* and the *General Electric Review*.[6]

The Tubes.—Figure 3 shows the special Phanotron and Thyratron tubes

that were used in this investigation. They are made entirely of iron, except for short glass tubes that support the anode and cathode. The construction of a mechanically strong seal between iron and glass was one of the major problems. It was solved by the development of a special alloy, called Fernico which can be sealed strain-free to an appropriate glass, and can be welded or copper soldered to iron. It will be noted that the Phanotron and Thyratron tubes are essentially alike except for the grid, which is an iron disc $^1/_8$" thick, welded to the iron envelope, bored with holes for the passage of electrons.

An important feature of these tubes is the thin-walled iron pipe at the bottom which holds the mercury, approximately 1 cc. This pipe or tubulation is so located that during operation its lower extremity is the coldest place in the tube, and hence controls the pressure of mercury vapor throughout the tube. A carefully ground valve confines the mercury within this receptacle during idle periods; it is held open by a thermostatic strip when the cathode is hot, but closes when the cathode is cold, thus preventing distillation of mercury to the cathode and walls of the tube.

Phanotrons and Thyratrons of this type are capable of operating satisfactorily at 15,000 volts at 200 amperes peak. A 12-phase rectifier unit, such as shown in figure 1, uses 12 such Phanotron tubes to change 200 amperes of alternating current to 200 amperes direct current at 30,000 volts; and the similar unit with 12 Thyratron tubes changes it back to alternating current. The tests indicate that the voltage of this unit may be doubled, trebled, etc., by using two, three, etc., tubes in series in place of each of the single tubes in figure 1; and the 30,000-volt unit equipments themselves may be connected in series to give any desired voltage.

The life of the Thyratron tubes requires provision for adequate electron emission, as has already been shown.[6] This is easily provided. In addition, life is found to depend markedly upon the circuit, which determines the velocity, and hence the destructiveness, of impacts of positive ions upon the anode. Circuit conditions have been found which minimize this effect, and promise a long tube life.

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CHIMPANZEE METABOLISM

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Read before the Academy, April 28, 1936

The respiratory metabolism has been studied with twenty-two chimpanzees selected from the breeding colony of the Yale Laboratories of Primate Biology, Inc., Orange Park, Florida. These animals, which ranged in weight from 2.9 to nearly 50 kg. and in age from 2 months to 15 years, were free from recognizable disease and were adequately fed and cared for. Under the captive conditions provided, the adults showed a record of successful breeding. The adults, with one exception, were captured in Africa, but the infants were born in captivity.

The respiratory exchange was measured with an open-circuit respiration chamber. A rotary blower drew outdoor air into the chamber and forced the outgoing air first through bottles of calcium chloride to remove water vapor, and then through a rotamesser or flow meter and over a sampling jet and finally through two 3-light dry gas meters to record the total volume of air leaving the chamber. During the experiment a proportional part of the outcoming chamber air was collected continuously in a sampling bag.[1] This air sample was subsequently transferred to a storage pump and later analyzed on the Carpenter gas-analysis apparatus.[2] The size of the respiration chamber varied with the size of the chimpanzee. A cage of steel window grills welded together was used inside the chamber for the adult animals. A small chamber without a containing cage was employed for the infants. Provision was made to record graphically the animal's activity throughout the experiment. To obtain periods uncomplicated by muscular activity, all measurements were carried out in the evening when the chimpanzee is usually asleep and quiet. Only the results obtained in periods of muscular repose are considered in the following analysis. The metabolic rate determinations were made usually after a fast of 12 hours, but in certain instances the fast was from 21 to 28 hours. The chimpanzee was placed in the metabolism cage and brought from its living quarters to the laboratory, where a temperature well within the subsequently established zone of thermic neutrality was maintained. It remained in quiet in the cage on the base of the respiration chamber for four hours before the experiment started. Rarely was the animal emotionally excited when placed in the cage.

Respiratory quotients of 0.78 and 0.74 were obtained after the fasts of 12 and 27 hours, respectively. These quotients indicate that the stimu-

lating action of food was not present during the measurements and, furthermore, that the chimpanzee approaches the post-absorptive state at least as quickly as and possibly more quickly than man.

Previous observation on the gaseous metabolism of the chimpanzee is limited to the measurements of three subjects by Bruhn,[3] who made no attempt, however, to study the factors related to changes in heat production. This present paper deals with the relation of environmental temperature, the menstrual cycle, sex, size and age, respectively, to the heat production of the chimpanzee.

The environmental temperature may have a pronounced effect upon the heat production of an animal. This is especially true in the case of the mouse, the rat and the pigeon, but with other animals such as the goose and the cow this factor does not play so important a rôle. Two chimpanzees living in unheated, but protected quarters during the Florida winter were able to withstand a temperature of 17°C. without an increase in heat production. Although one chimpanzee had a good coat of hair and the other a sparse covering, the poorly covered animal reacted no more to the low temperature than the animal with the good coat of hair. This indicates that at environmental temperatures of 17°C. or above the covering of hair on the chimpanzee plays little or no part in the conservation of heat. Other chimpanzees, which lived in heated quarters during the winter months and hence were not inured to the cold, showed an increase in the metabolic rate between 17° and 20°C., but above 20°C. and up to 29°C. the heat production was at a minimum. The range of temperature within which the heat production of the chimpanzee is at a minimum level is, therefore, fairly wide and corresponds closely to the zone of thermic neutrality for man.

The metabolism of two mature female chimpanzees was studied at thermic neutrality on alternate days during two complete sexual cycles, with the object of determining the relationship of the menstrual cycle to the heat production. Both females had given birth to normal infants and had cared for them for about one year. These two animals were considered to be representative of normal chimpanzees, though they differed in some respects. Josie, who weighed about 39.5 kg., had a fairly good covering of hair, whereas her cage mate Wendy, weighing about 35 kg., was entirely bare of hair in spots. Wendy, in contrast to Josie, has always shown a greater degree of sexual activity and has a shorter sexual cycle (35 days) than Josie (40 days). The 24-hour heat production of Wendy during the first 10 days of the cycle (the first day of bleeding being considered the first day of the cycle) was significantly lower than that during the remaining days of the cycle, averaging 884 and 957 calories, respectively, per 10 times the two-thirds power of the weight. Josie did not have a low metabolic rate during the first 10 days of the cycle, but her

metabolism did undergo a decrease between the 20th and the 30th day. The average heat production during the first 20 days and the last 10 days of her cycle was 943 calories and that for the 20th to the 30th day was 919 calories per 10 $w^{2/3}$.

With both these chimpanzees low values of about 850 calories were obtained on several days, and high values of slightly over 1000 calories on several other days. The average value for all the days when Wendy was studied is 939 calories, the average in Josie's case is 936 calories. Inspection of the results indicates that, although the metabolism of the female chimpanzee is subject to considerable variation from day to day, a series of determinations made over a period of two weeks will give an average value close to that obtained in observations extending over one or two months. However, in experiments designed to study the effect of some factor superimposed upon the basal metabolism, especially when the effect is small and subtle, the average value of a series of metabolism measurements made over an extended length of time cannot be used as the base-line, because of the possible magnitude of the variation in the metabolism from day to day. Rather the basal heat production should be determined immediately before such an experiment.

On the basis of experience with man, one would not expect a sex difference in the metabolism of young animals. In our study of the heat production of four infant male and four infant female chimpanzees we have found no evidence of a higher metabolism in the males than in the females. Among humans, the metabolism of women is about 7 per cent lower than that of men. The metabolic rate of the 7 adult female chimpanzees that were studied averaged 993 calories per 10 $w^{2/3}$ and that of the two adult males 999 calories, a value nearly equal to the rate of the females. However, the data for the males are not sufficient to establish, with any degree of reliability, the average metabolism of this sex.

With the chimpanzee, as with other animals and man, the larger animal has the greater heat production. Among the males, for example, the range in the average *total heat production per 24 hours* was from 226 calories by a chimpanzee weighing 2.9 kg. to 1227 calories by a chimpanzee weighing 48 kg. However, the smaller animal has a greater heat production per kilogram of body weight than the heavier animal, the range for the males being from 76.8 calories for the 2.9-kg. chimpanzee to 25.6 calories for the 48-kg. chimpanzee. In contrast, the 24-hour heat production referred to the two-thirds power of the body weight times the factor 10 is singularly uniform for chimpanzees of vastly differing weights and of both sexes, averaging 980 calories (measured at thermic neutrality).

Since this last method of expressing the heat production is commonly employed to minimize any rôle played by differences in the sizes of animals, we may examine the data thus expressed to note whether the factor of age

has any effect upon the metabolism. Only one chimpanzee at the age of 2 to 3 months was available for study. The average heat production of this infant was 1104 calories. Six chimpanzees one year of age, weighing from 4 to 7 kg., had a fairly constant heat production averaging 975 calories. With adolescent chimpanzees weighing 25 kg. and adults weighing over 30 kg., values closely approximating 1000 calories were found. It is concluded that the chimpanzee, unlike man, does not have an extremely high intensity of metabolism per 10 $w^{2/3}$ in infant and pre-adolescent years.

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A DETERMINATION OF THE MAGNITUDE OF THE CELL "SENSITIVE VOLUME" ASSOCIATED WITH THE WHITE-EYE MUTATION IN X-RAYED DROSOPHILA—II

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Communicated May 13, 1936

In a previous communication[1] we described the methods used and the results obtained in a probability determination of the magnitude of the volume and radius of the cell "sensitive volume" associated with the mutation to white eye in *Drosophila melanogaster*, and pointed out that such a figure might be tentatively interpreted as the minimum limiting value for the size of a gene. More recently additional work has been completed giving a more reliable determination of this figure. The order of magnitude of the volume is not essentially changed.

Two of the points on the curve of percentage mutation against x-ray dosage have been independently re-determined by one of us, using a new stock of eosin, furnished by Turtox Service. One new point, at an exposure of one-quarter minute, has been added. The x-ray conditions have been maintained identical with those earlier described, a similar tube being used. The earlier and later values of the re-determined points differ by less than their respective probable errors as given in the earlier paper. Thus the earlier determination of the percentage of affected eyes at an exposure of one minute was 0.52 per cent, the later, 0.48 per cent; the respective corresponding values at the four-minute point were 2.14 per cent and 1.63 per cent.

Table 1 gives a summary of all the data obtained (for males only).

TABLE 1

EXPOSURE	TOTAL NUMBER OF EYES[1]	NUMBER AFFECTED	PER CENT AFFECTED	PROBABLE ERROR (PERCENTAGE)	CALCULATED TOTAL SENSITIVE VOLUME
Control	3143	0	0.00		
1/4 min.	1716	2	0.12	±0.057	35.16×10^{-18} cc.
1/2 min.	2884	8	0.28	±0.075	41.18×10^{-18} cc.
1 min.	4616	23	0.50	±0.070	36.76×10^{-18} cc.
2 min.	2114	18	0.85	±0.135	31.25×10^{-18} cc.
3 min.	1740	26	1.49	±0.195	36.52×10^{-18} cc.
4 min.	2215	38	1.72	±0.185	31.62×10^{-18} cc.

[1] It will be noticed that the total number of eyes given is sometimes odd. This situation results from the method used in counting. To facilitate rapidity, one eye only of each fly was counted in many cases. This, because of the random distribution of modified patches in right and left eyes, is considered a justifiable procedure.

The plot of percentage affected eyes as a function of exposure time (Fig. 1) is such, as in the earlier determinations, that a straight line may be considered the best fit for the seven points available. This permits a calculation similar to that described previously,[1] yielding the values given for the average total volume of loci for white in a single anlage. The weighted mean of these values, calculated according to the percentage probable errors of the observations, is 36.20×10^{-18} cc. This number may be considered to represent the lower limiting value of the total volume of the white loci in the x-chromosomes of all cells of an optic anlage at the time of treatment; the value previously obtained[1] was 36.40×10^{-18} cc.

In the earlier work the assumption had to be made that propagation of affected and unaffected cells of the anlage was comparable in rate, so that the number of cells present in the primordium of the eye at the time of irradiation could be represented as the ratio of the number of affected ommatidia to the total number present in the mature organ. Such an assumption is unsatisfactory for a number of reasons; we have therefore made a careful study of the cytology of the optic anlage in the larva of Drosophila, leading to a direct count of the number of elements present in the optic anlagen of larvae of the ages x-rayed. The details of the cytological work are published elsewhere.[2]

Averages of cell counts from the best slides obtained, of sections made perpendicular to the long axes of the element of the anlagen, gave 15.6 as the mean best figure for the cell number in the primordia of larvae between eighteen and twenty-four hours after laying.

On this basis the average volume of the individual locus for white eye was calculated as 2.32×10^{-18} cc. The corresponding radius, assuming the locus to be spherical in form, is 8.21×10^{-7} cm. The curve of the number of cells in the optic anlage as a function of age of the larva rises extremely

steeply in the region where we worked,[2] so that a few hours will make a very large difference in the number of cells observed, and only the order of magnitude may be considered of significance. It is to be seen that the refinements introduced have not modified earlier results to a marked degree; the figure previously given was 7.62×10^{-7} cm. Both values, as indicated for the latter in the earlier communication,[1] lie reasonably close to those determined by other methods by Morgan,[3] Blackwood[4] and Gowen and Gay.[5] They also agree rather well with Marshak's result in *Gasteria*.[6]

It is interesting to compare this value with the dimensions of enzyme and protein molecules. The insulin molecule has a diameter of 4.36×10^{-7} (Sjogran and Svedberg, 1931), trypsin 5.2×10^{-7} cm. (Northrop and Kunitz, 1932), haemocyanin 2.4×10^{-6} cm. (Svedberg and Chirnoaga,

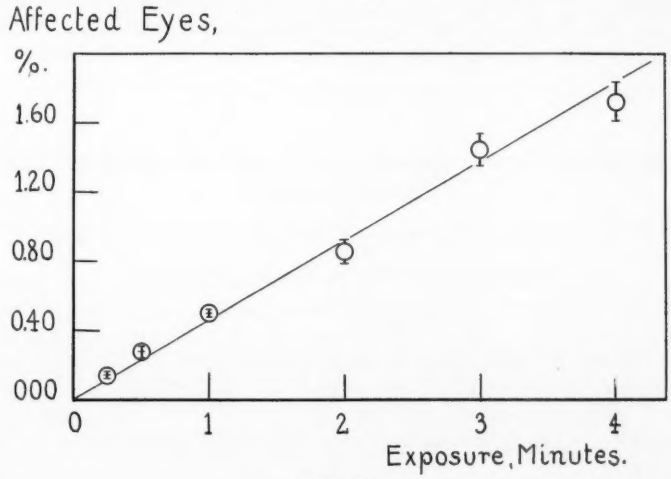

FIGURE 1

1928) and albumen 4.34×10^{-7} cm. (Svedberg and Sjogran, 1929; Nichols, 1930). The agreement in order of magnitude may prove suggestive in considerations of the structure of the gene.

Throughout this work, only data from males have been considered in calculation. It has been found that females show substantially the same number of single locus modifications as males under comparable exposures. Modifications in the female take the form of light patches of male-color tissue superposed upon the darker female-color background, since eosin is bicoloric. The counts for females have been sufficiently verified independently to cast doubt upon their basis in error of observation. Since the character eosin is represented by two loci in the female (both *X*-chromosomes) and but one in the male, this represents a result anomalous on

purely probability considerations, and the question requires further investigation. Recently we have found a limited number of irradiated females in which both loci were apparently simultaneously affected, resulting in patches of whitened ommatidia, identical with those found in the male, superposed upon the dark eosin background. Such occurrences are very infrequent, so that the examination of an extremely large quantity of material is required for their study. A statistical investigation has been undertaken of the distribution of these "double-white" mutations in diploid stock, and of their occurrence in triple-X stock, and may shed some light on this phase of the question.

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DARK ADAPTATION AFTER VARYING DEGREES OF LIGHT ADAPTATION

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Communicated May 13, 1936

The photosensitive system of a photoreceptor must involve at least two processes, a light-sensitive process and a recovery process. Arnold and Winsor (1934) have shown that the validity of Talbot's law implies that the velocity of the light-sensitive process is directly proportional to light intensity.

In the further analysis of the photosensitive system the most direct line of attack seems offered by a study of dark adaptation. One adapts the eye to a given intensity of light, extinguishes the adapting light, and then determines the threshold intensity as a function of time in the dark. If the threshold intensity is a measure of the concentration of photosensitive material present, we have a means of studying the recovery process. Unfortunately, we do not know the nature of the relation between threshold and concentration of photosensitive material; but even without such knowledge some progress is possible.

We may write the equation for the rate of change of the photosensitive material S in the form

$$\frac{ds}{dt} = -I\phi, (s, x, y \ldots) + \phi_2 (s, x, y \ldots) \qquad (1)$$

in which the first term on the right represents the light-sensitive process, and the second the recovery process. The variables $(x, y \ldots)$ we assume to be completely determined by the distribution of material in the photosensitive mechanism at any time; or, we may take $(x, y \ldots)$ to be actually the values of the various concentrations.

Let us now assume further that a cyclic mechanism will describe the system, in which some fixed amount of material is distributed between various states, of which $(s, x, y \ldots)$ are the amounts. Evidently, then, if there are n states, there will be $(n - 1)$ variables entering in the right-hand side of (1); and, in general, we shall require $(n - 1)$ differential equations for a complete description of the system.

The theoretical treatment of photoreception given by Hecht (1934) assumes that only two states exist; that the photosensitive substance S is broken down to P, and that S is reformed directly from P. In this case (1) simplifies to

$$\frac{ds}{dt} = -I\phi_1(s) + \phi_2(s). \tag{2}$$

If now we consider the course of dark adaptation subject to (2) we have

$$\int_{s_0}^{s} \frac{ds}{\phi_2(s)} = t - t_0. \tag{3}$$

From (3) it appears that recovery curves for a single receptor element, or for a homogeneous population of elements, from different initial conditions will differ only in their position on the time axis. If, then, one light-adapts to a series of different intensities, one should obtain a series of dark adaptation curves starting at different levels, but superimposable by a shift on the time axis.

Experiments of this kind have been reported by Blanchard (1918) for the eye as a whole, and by Fedorova (1927) and Johannsen (1934) for the fovea. In all cases the curves differ in shape for different initial adapting intensities. In the belief that possibly the experimental technique hitherto used was not completely satisfactory, experiments have been undertaken to test the point.

The observer was light-adapted for five minutes by an opal glass field 18×24 cm., about 4 cm. from the eyes; the illumination on the adapting field was from a 1000w projection lamp, variable in position to regulate the adapting intensity. To provide greater range in the adapting intensity, a screen with a smaller opening covered with opal glass was inserted in front of the adapting screen.

Threshold measurements were made on a circular test patch subtending, in one series 1.3° of visual angle, in a later series 0.44°. A fixation point was located at 9.8° from the center of the test patch. Observations were

made monocularly with the natural pupil; provision was made in the apparatus for observation with either eye, and as a general rule the course of adaptation in both eyes was followed. The test patch was exposed through a camera shutter operated by the observer, set at $^1/_{50}$ second. The illumination on the test patch was provided by the adaptometer described by Derby, Chandler and Sloan (1929), which we calibrated over a range of intensities from 0.22 ml. to 0.000075 ml. (For the use of this instrument we are indebted to the kindness of Dr. J. Herbert Waite.)

A typical set of curves is shown in figure 1. It will be noted that at the

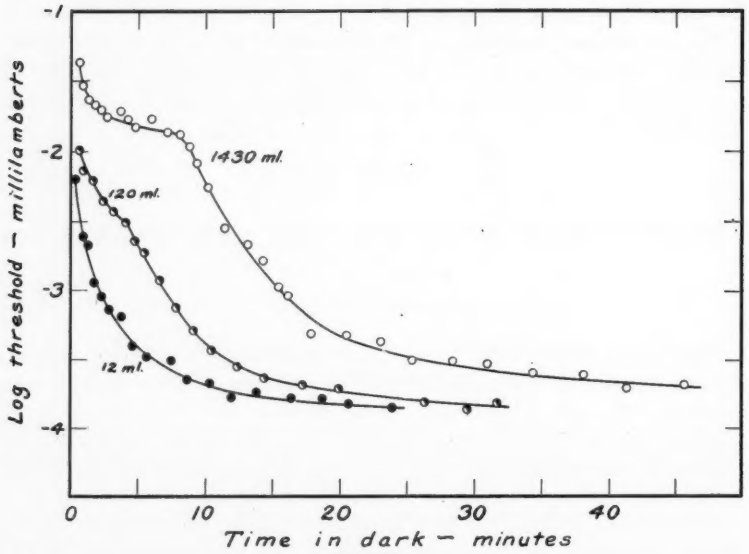


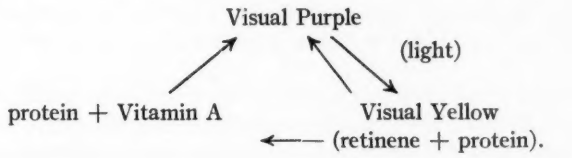
FIGURE 1

Dark adaptation following 5 minutes light adaptation to indicated intensities. (Curves obtained on left eye of C. P. W.; test field 1.3° visual angle.)

highest intensity there is a clear separation into cone and rod adaptation curves, as has been found by Kohlrausch (1922, 1931), Hecht, Haig and Wald (1935) and Hecht and Haig (1936). We may here confine ourselves to the rod curves (the lower portions, subsequent to the break). It is apparent that the curves are of markedly different shapes, and that they are not superimposable by any shift on the time axis. Figure 2 shows curves in which the two eyes were simultaneously adapted to different levels, by the use of a filter covering one eye during adaptation. Here again the difference in shape is evident.

It is thus apparent that equation (2) cannot be adequately descriptive of

the facts. Of the assumptions involved, the most obviously questionable seems to be that of the existence of only two states for the photosensitive material. Wald (1935a, b) has given strong reasons for supposing that the chemistry of the visual purple cycle involves at least three substances, in the form:



(4)

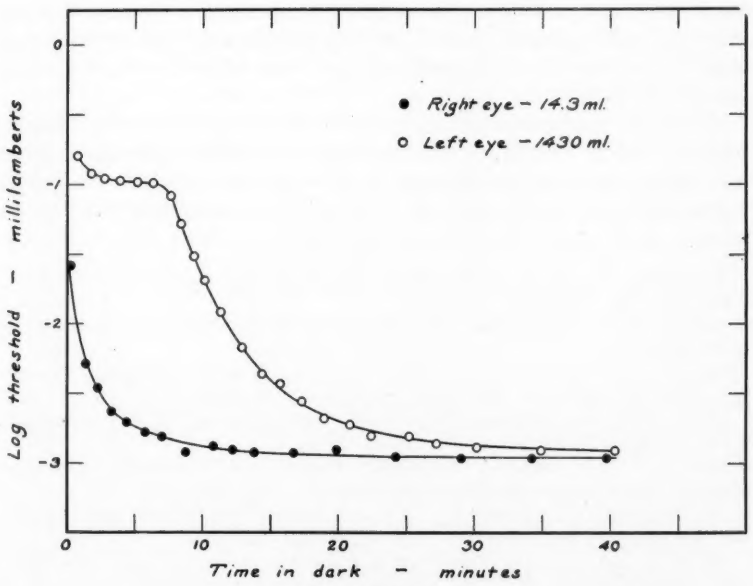


FIGURE 2

Dark adaptation following simultaneous light adaptation of right and left eyes to indicated intensities. (Observer A. B. C.; test field 0.44° visual angle.)

It is clear that if (4) represents the chemical situation, our equation for rate of change of S cannot be written as in (2), but must be written

$$\frac{ds}{dt} = -I\phi_1(s, x) + \phi_2(s, x) \qquad (5)$$

since now three states rather than two are involved.

Further, the course of recovery will depend not only on the total amount

of visual purple which has been changed, but on its distribution between visual yellow and vitamin A; and this distribution need not be independent of the adapting intensity.

Attention should here be called to experiments by Wald and Clark (1936) in which differences in the form of the dark adaptation curve are obtained by varying the *time* of light adaptation. These differences are in complete agreement with what would be predicted from the chemical scheme (4).

No attempt is here made at a further analysis of the curves obtained, because, in the absence of independent evidence as to the orders of reaction and the magnitudes of the velocity constants, the possibilities available are so wide as to render any curve fitting a meaningless procedure. It is, however, quite possible that a suitable experimental procedure would separate the reactions and enable one to obtain curves in which a single reaction predominated.

Summary.—The shape of the human dark adaptation curve changes with changes in the degree of initial light adaptation. The changes are inconsistent with the assumption of a mechanism in which the active material exists in only two states. The results are consistent with Wald's mechanism in which three states are postulated.

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STUDIES ON THE BODY TEMPERATURES OF ELEPHANTS

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Body temperature signifies to most of us a temperature of 98.6°F., as we are accustomed to looking for this particular temperature on the ordinary clinical thermometer. The temperature of the body, however, is seldom precisely at this level always, but even with humans it undergoes a considerable daily rhythm, with a minimum somewhere between 12 midnight and 6 A. M. and a maximum at about 4 to 6 P. M.[1] In comparative physiology one of the factors of great importance is the body temperature, as this represents the balance between heat production and heat loss. The temperature-regulating mechanisms of different animals are obviously not exactly the same. The small, well-furred mouse, which has in proportion to its weight a much larger surface area for heat loss, must have a differently functioning mechanism from that of the enormous elephant with its relatively small surface area in proportion to its weight and its lack of fur protection. The physiology, as a whole, of the elephant has been but slowly approached by physiologists. In a recent survey by the Nutrition Laboratory of the physiology of the elephant,[2] largely centered upon one 4000-kg. adult female, but supplemented by observations on 62 other elephants, a careful study was made of the body temperature.

Although the body temperature of the elephant has been recorded in the literature, notably in the authoritative book by Evans,[3] amazingly little is known about its body temperature by the men in charge of such animals in American zoölogical parks and circuses. Few of these men have ever taken the body temperature of the elephant or know precisely what it is. Fortunately elephants are singularly free from disease, except for furunculosis, and hence there has been no imperative need for temperature measurements. A physiological survey of the elephant, however, cannot disregard body temperature. The method used in India for determining the elephant's body temperature is to have a mahout, holding a thermometer in his hand, insert his well-lubricated arm deep into the capacious rectum, after first removing several of the huge balls of feces. This method is impracticable for general use, and measurements of the elephant's rectal temperature are seldom attempted at the present day. However, there are two excretory products periodically discharged by the elephant, the temperatures of which may serve as a close index of the internal body temperature. These are the urine and the feces which, because they have been residual deep in the abdominal cavity for some time before being discharged, must assume the body temperature. As

the volume of urine voided by the elephant at one time averages $5^1/_2$ liters and may amount to as much as 9 or 10 liters, the initial thought of Stephen Hales[4] in 1731 of obtaining an indication of the body temperature by measuring the temperature of a stream of urine would be applicable in the case of the elephant. The fecal discharge of the elephant is likewise large, five or six boluses being passed, on the average, at one time, each weighing from 1 to 2 kg. The temperatures in the centers of these huge balls should at least approximate the internal temperature of the body.

Temperature of the Urine.—The determination of the urine temperature is simple. A wide-mouthed thermos jar (500-cc. capacity) is filled with water at approximately 37°C. The moment the elephant begins to urinate, this water is thrown out and a jarful of urine is collected. Usually the discharge is so voluminous and so prolonged (several seconds) that the first jarful can be thrown out and the jar refilled, which enables a still more accurate measurement of the temperature of the urine. An ordinary clinical thermometer is then thrust into the urine, and the temperature is read within one minute. Such records were obtained with 45 elephants, and many times with one particular elephant. The constancy in the body temperature of the elephant is perhaps closer than that found with humans, as is shown by the data in table 1, which represent typical measurements of the urine temperatures on the same day with the same elephant. Between April 2 and April 11, seventy-three specimens of urine were collected,

TABLE 1

TEMPERATURES OF THE URINES OF A 4000-KG. ELEPHANT

(April 9, 1935)

TIME OF DAY	BARN TEMPERATURE, °C.	WEIGHT OF URINE COLLECTED, KG.	URINE TEMPERATURE, °C.
1:33 A. M.	11	3.35	35.8
2:50 A. M.	10	3.15	36.0
6:27 A. M.	10	8.74	36.0
9:26 A. M.	9	5.10	35.8
11:36 A. M.	9	3.29	36.0
4:55 P. M.	13	5.65	35.6
6:32 P. M.	11	4.81	35.5
8:54 P. M.	9	10.72	36.1
11:02 P. M.	9	3.40	35.9

the temperatures of which were recorded. These exhibited an extreme range of from 34.4° to 36.5°C. After the first three days, when the technique was perhaps not quite so perfect as during the remainder of the time (that is, between April 5 and April 11, when fifty-two urine temperatures were measured), the range was only from 35.0° to 36.5°C. In general, the widest range was not far from 1°C., as is shown by the comparisons in table 2. The average urine temperature during the entire

series of observations on this particular elephant was 35.6°C. With 30 elephants of the Ringling herd, urine specimens were obtained usually only once in each case, occasionally twice. The minimum temperature noted with this herd was 35.4°, the maximum 36.3° and the average 35.8°C., or almost identical with that found in the more detailed study with one elephant. With 11 elephants of the Al G. Barnes herd a minimum temperature of 35.7°, a maximum of 36.2° and an average of 35.9°C. were recorded. The average body temperature of the elephant may, therefore, be considered to be 35.9°C.

TABLE 2

MINIMUM, MAXIMUM AND AVERAGE TEMPERATURES OF THE URINE OF A 4000-KG. ELEPHANT

DATE 1935	MINIMUM °C	MAXIMUM °C.	DIFFERENCE °C.	AVERAGE °C.
April 2	34.6	35.3	0.7	34.9
April 3	34.4	36.0	1.6	34.9
April 4	34.8	36.0	1.2	35.5
April 5	35.5	36.5	1.0	35.9
April 6	35.1	36.2	1.1	35.8
April 7	35.2	35.9	0.7	35.7
April 8	35.0	36.0	1.0	35.5
April 9	35.5	36.1	0.6	35.8
April 10	35.5	36.2	0.7	35.9
April 11	35.1	36.0	0.9	35.6
Average				35.6

Temperature of the Feces.—As the feces likewise represent a large mass with a large water content deep in the body cavity, one would expect that the temperature of the interior of a ball of feces should also represent the body temperature. This temperature was technically even easier to obtain than the urine temperature, and an extensive study was, therefore, made of the temperatures of balls of feces immediately after they were passed. Although the exterior of the bolus was cooled in the air, the interior held its temperature longer. The procedure finally used was to insert an ordinary clinical thermometer 2 or 3 cm. into a ball of feces the moment it was passed, leave the thermometer there for half a minute, then push it in another 2 or 3 cm., and after a further $1^1/_2$ minutes record the maximum reading. When the thermometer is inserted the first few centimeters, it is warmed from the temperature of the air to approximately that of the feces, and when it is inserted farther, the true temperature of the feces is obtained. Invariably the feces temperature was found to be notably higher than the urine temperature, on the average 0.7°C. At first this discrepancy was difficult to explain, but it soon became clear that this was the direct effect of the fermentation processes, that fermentation was still

taking place in the ball of feces, and because of its solid structure (in no sense semi-fluid), its temperature could not be rapidly equalized.

The recommendation is made to practical elephant men and zoölogical park directors that the temperature of the elephant may be rapidly and accurately obtained by taking the temperature of the feces as indicated above and deducting 0.7°C. from the reading obtained. Rarely should the temperature found be significantly different from 35.9°C. In those rare cases where such values are not obtained, further readings must be made and the real difference established. Since with the elephant defecation occurs about 14 or 15 times a day and can frequently be stimulated by suggestion, this method of determining the body temperature presents no difficulty.

Most mammals have a body temperature not far from 35° to 41° or 42°C., birds having the highest temperatures. The smaller mammals, such as the rat and the mouse, likewise tend to have a fairly high temperature. Man has a relatively lower temperature of about 37°C., although there are daily fluctuations, as previously mentioned. The large farm animals have notably higher temperatures. It is surprising, therefore, that the elephant, nearly the largest mammal and an animal whose heat production has been found to be the greatest in proportion to its surface area of any animal that the Nutrition Laboratory has thus far studied, has the lowest body temperature of any of the large animals.

[1] Benedict, F. G., and Snell, J. F., *Arch. ges. Physiol.*, **90**, 33 (1902); Benedict, F. G., *Am. Jour. Physiol.*, **11**, 145 (1904).

[2] The details of this investigation are being published in monograph form by the Carnegie Institution of Washington (Publication No. 474, "The Physiology of the Elephant," by Francis G. Benedict).

[3] Evans, G. H., *Elephants and Their Diseases*, Rangoon (1901 and 1910).

[4] Hales, Stephen (cited by Pembrey, M. S., *Schäfer's Text-Book of Physiology*, London, 1898, **1**, p. 786, footnote 2).

DIFFERENTIAL SENSITIVITY IN SOUND LOCALIZATION

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In the study of the physiology of the central nervous system a method is desirable which will permit measurement of phenomena which can be precisely controlled as functions of known physical variables. The integrative rôle of the central nervous system in behavior has been continually stressed since Sherrington first elaborated the idea. An intact living animal is constantly under the influence of a multiplicity of forces deriving from energy changes in its environment. These forces, through the mediation of receptors and sensory nerves, converge upon the central nervous system where integration occurs. The observable result is an event which we term a response, the essential characteristic of which is its unitariness. Properties of these unitary responses can in many instances be measured, but only under the most favorable conditions can the factors determining the response be dealt with as measurable quantities.

Loeb[3] discussed several examples of behavior which result when several forces act simultaneously upon an animal, and it seems sensible to assume that the function of the central nervous system as an integrating mechanism is concerned when several different forces act to determine behavior. Crozier[2] and his collaborators have extended the method of tropistic analysis in interesting ways to deal with several forms including young mammals. The method utilized in these cases has the distinct advantage of permitting determination of the function relating response to the governing physical forces, and consequently the activity of the central nervous system as an adjustor mechanism.

A method was sought which would permit the examination and description of central nervous activity in the human subject, involving unitary response to multiple stimulation deriving from separate peripheral fields.

The phenomena involved in the binaural localization of sound when the two ears are stimulated differentially as regards the dimension of energy,[1] apparently supply such a method. When the energies of stimulation at the two receptors are equal the apparent sound is localized at the midpoint of a line passing through the two receptors and perpendicular to the median vertical plane of the head. Adequate change of the energy of stimulation at one of the receptors causes the position of the apparent sound to shift from the median plane toward the receptor receiving the greater stimulation. It is necessary to change the energy of stimulation at one ear by an adequate amount before any change in the apparent position of the synthesized sound can be detected. This quantity can be determined as a function of the fixed energy at the other ear.

A Beat Frequency Oscillator (General Radio Type 614) was used as a source of sound. The output of the Oscillator was amplified by a two-tube resistance-capacity coupled amplifier. The output of the amplifier was

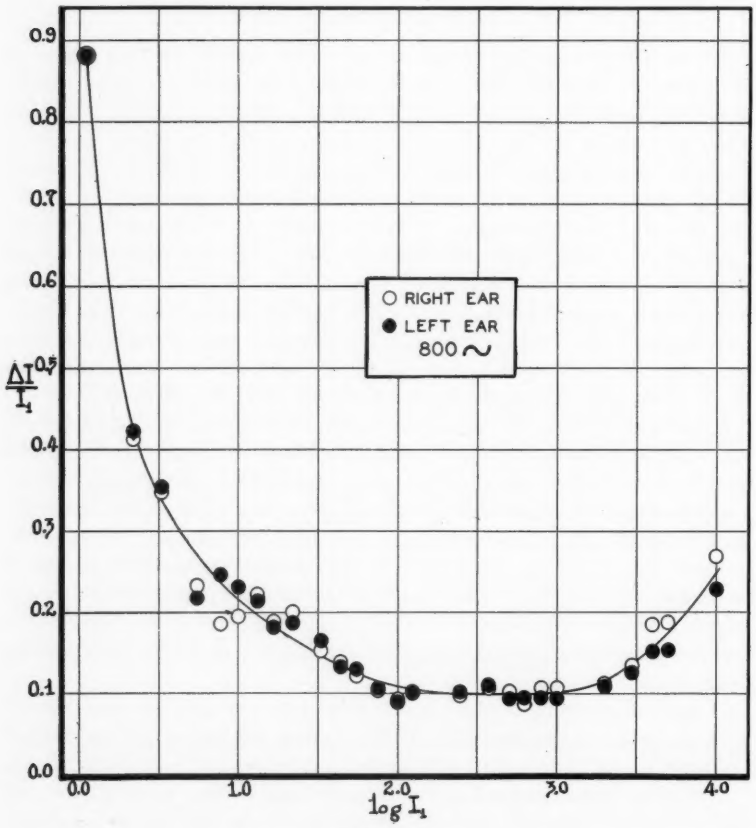

FIGURE 1

The values of $\Delta I/I_1$ for the lower and intermediate levels of intensity correspond rather closely with the values obtained by Reisz[4] at this frequency; he employed a "method of beats" in the determination of the curve describing differential intensity sensitivity of the ear for pure tones. The curve presented here shows a rather rapid increase in the value of $\Delta I/I_1$ for the upper levels of intensity. The reason for this is not at present apparent.

split and led to the grids of two power tubes which actuated two magnetic loud-speaker units arranged as headphones. The relationship between the electrical energy actuating the headphones and the acoustic energy de-

veloped by them was determined by means of a calibrated microphone and was found to be rectilinear over the range of energies involved in the experiment. Volume controls ahead of the power tubes made possible independent control of the energy actuating each speaker, without changing the energy actuating the other speaker. The voltages at the speakers were measured with a high resistance type voltmeter. Low voltages were amplified by a calibrated amplifier to bring them into the range of the voltmeter. When the voltage readings at the speakers were equal the sound appeared to be located centrally between the two receptors.

Ten determinations of the increase in voltage just necessary to cause a shift of the sound from the median position were made for each receptor at a frequency of 800 cycles. The determinations were made at several voltage levels (I) ranging from somewhat above the lower threshold to the approximate "threshold of feeling." In terms of voltage the levels of stimulation ranged from 0.001 to 10 volts. In each determination the fixed voltage $= I_1$, the voltage just producing recognizable shift $= I_2$.

When the mean voltage increments ($\Delta I = I_2 - I_1$) just sufficient to produce an apparent shift of the sound from the median plane at various levels of I_1 are plotted as in figure 1, $\Delta I/I_1$ *vs.* $\log I_1$, the curve is of the familiar type which commonly describes the differential intensity sensitivity of animals where determinations are made over a wide range of energy values. In the lower range values of ΔI are large, gradually declining and increasing again when the level of stimulation is high. It is obvious that the measurements are not describable in terms of the Weber-Fechner Law. The ratio $\Delta I/I_1$ is in no sense constant but passes through a wide range of values depending on the level of stimulation at which a determination is made. The variation of the determinations varies with the level of stimulation, increasing as the level of stimulation increases. A discussion of the theoretical implications of the results presented will be offered in a paper to be published later.

Summary.—Binaural localization of sound is a case where a unitary measurable response can be dealt with in its functional relationship with the determining physical factors. When two ears are stimulated by equal energies at a frequency of 800 cycles the apparent sound is localized in the median plane of the head. When the increments of energy necessary to cause a just noticeable shift of the localization of the apparent sound from the median plane are determined for a wide range of energy levels, the ratio $\Delta I/I_1$ is found to be large for low levels of energy, small for intermediate levels and to increase for very high energy levels. When the ratio $\Delta I/I_1$ is plotted against $\log I_1$ the resulting curve is of the type which commonly describes differential intensity sensitivity.

[1] Boring, E. G., "Auditory Theory with Special Reference to Intensity, Volume and Localization," *Am. Jour. Psychol.*, **37**, 157–188 (1926).

[2] Crozier, W. J., and Pincus, G., "Tropisms of Mammals," *Proc. Nat. Acad. Sci.*, **12**, 612–616 (1926).

[3] Loeb, J., *Forced Movements, Tropisms and Animal Conduct*, J. B. Lippincott Co. (1918).

[4] Riesz, R. R., "Differential Intensity Sensitivity of the Ear for Pure Tones," *Phys. Rev.*, **31**, 867–875 (1928).

ON THE SENSORY DISCRIMINATION OF INTENSITIES

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Although the relationship between sensory intensity and physical intensity of the excitatory agency cannot be directly established, it is possible to measure properties of the process whereby sensorial discriminations of differences of intensity are achieved. This is the classical problem of psychophysics. It is also a type problem for experimental biology. In general, as in the case of sensory intensity, the nature of the event or process which controls and determines a particular sort of regularity in the performance of an organism is not open to direct examination; it must be inferred from its quantitative properties. Inferences of this sort are likely to be based upon the use of averages of measurements of performance. An examination of the properties of the data of intensity discrimination indicates that such use of averages may be misleading, significantly in the sense that it involves ignoring a large part of the really useful information the measurements give. Averaging is commonly employed as a means of overcoming variation in the individual measurements. This variation, however, in homogeneous series of measurements, is a definite property of the reacting or performing organism, and cannot be dismissed as "experimental error"; its laws are discoverable, and describe an essential aspect of the process by virtue of which the measurements arise.[1] A homogeneous series of measurements is one involving equal numbers of measurements on each organism at various values of the inciting variable, based upon the performance of either (*a*) a single individual, within a period in which the absence of irreversible spontaneous or other changes in capacity for performance is demonstrable; or (*b*) a group of individuals genetically alike and otherwise demonstrated to be effectively equivalent for the purpose of the measurements.[2,1]

Data upon intensity discrimination already exist, and have recently been added to, which satisfy these criteria of homogeneity. The usual and traditional form of these data consists in the statement of values of the Weber

Fraction $\Delta I/I_1$ as a function of I_1; I_1 is a given intensity of the excitatory agent (e.g., light), such that $I_1 \pm \Delta I$ is just determinably different from I_1. The magnitude and the properties of ΔI depend, for a given I_1, upon the procedure employed in comparing I_1 and $\Delta I \pm I_1$. When I_1 is any fixed value of I and values of $I_2 = \Delta I + I_1$ are found by continuously increasing I_2, then ΔI is observed to be really a simple function of I_2 rather than of I_1. Log ΔI is a rectilinear function of log (means I_2), and ΔI of

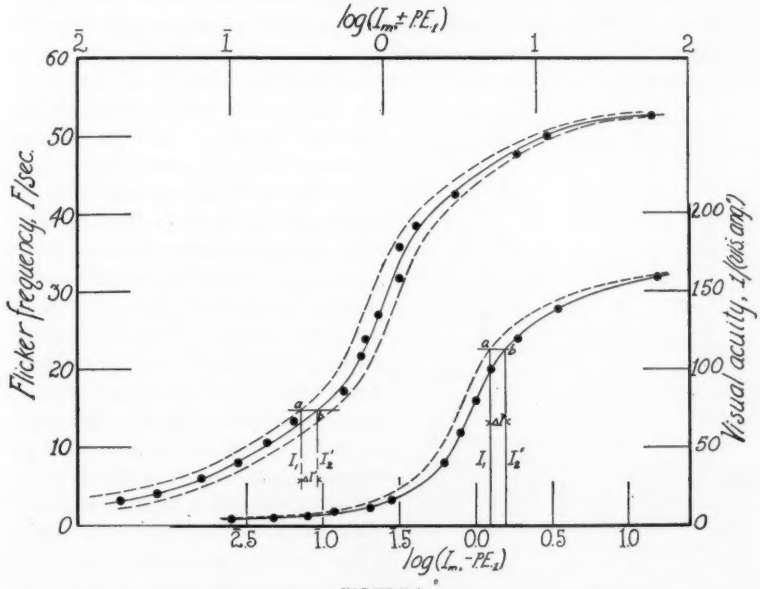

FIGURE 1

The curves of response to flicker, and of visual acuity, derived from data on the bee.[6,5] The observations are of mean intensities (I_m) to give reaction at fixed levels of F or of $V.A.$, together with P.E.$_{I_I}$. The band is drawn to enclose $I_m \pm$ P.E.$_{I_I}$. The line ab defines the level of F or of $V.A.$ distinguishable from the range associated with I_1, and thus gives I_2'; $I_2' - I_1 = \Delta I'$.

$\sigma_{\Delta I}$ (i.e., of σ_{I_2})[3]; in homogeneous series of tests mean I_2 is directly proportional to σ_{I_2}.

The vast literature of the Weber-Fechner discussion has been centered upon the alleged or expected constancy of the ratio $\Delta I/I_1$, and only to a small extent has it dealt with the physical nature of the discriminable increment of intensity, ΔI. We have to inquire if the proportionality between ΔI and σ_{I_2} does not mean that two just discriminable intensities, in the procedure indicated, are distinguished by what is in effect an elementary

statistical process. Two intensities are not compared; their *effects* are, and these effects are variable. The action of a fixed I_1 is certainly variable from moment to moment; the array of effects (sensory) due to I_1 is compared with the effects due to various I_2's; the mean value of the just detectably higher I_2 defines ΔI; it is reasonable to expect that ΔI should be determined by properties of the two frequency distributions.

The question must be approached empirically. It involves determining the law of the *variation* of effect (E) as a function ofi ntensity, as well as the law of variation of intensity I to produce different constant levels of an effect not directly accessible to inspection.[1] By means of experiments in which another coördinate of reference is employed, however, it is possible to verify the expectations of the general argument. One set of such experiments is here considered.

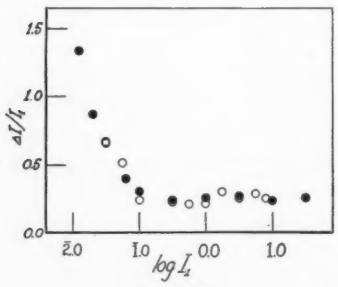

FIGURE 2

The ratio $\Delta I'/I_1$ computed as in figure 1 is identical in the two cases; solid circlets, from the flicker curve, open circlets from the visual acuity curve.

Independent determinations of intensity discrimination,[4] visualacuity,[5] and flicker recognition[6] have been made with bees by the method of obtaining threshold responses to a moving stripe-pattern. These determinations, which satisfy the criteria of homogeneity, all show that I_2 and σ_{I_2} are directly proportional within each series.[7] It should then be possible to calculate from the measurements of visual acuity and of flicker response a ΔI having the same quantitative properties as that determined directly. The procedure amounts to asking the bee to make for us an intensity discrimination by means of the properties of its flicker response curve or of its visual acuity curve. This is not unreasonable, since the reactions utilized,[7] as in all visual tests, depend fundamentally upon intensity discrimination (as pattern in space, in time, or both). The calculation is made graphically, and is based upon recognition of the fact that the observations are properly described not as a curve but as a band giving the dispersions of the measurements (and thus the observed probability of the response upon which the measurements rest). To attempt to deal merely with average values of I_2 by the method of fitting a theoretical equation encounters the very serious difficulty that if the curve, of flicker response for example, be determined by measuring mean flicker frequencies at fixed intensities the two curves are predictably not identical and the same criteria of curve fitting cannot be employed.[8] The reason for this is that the organism's index-reaction is the result of the effect of the play of a given

intensity I upon a mechanism inherently fluctuating in its capacity to give the critical response. (Identical considerations apply, as the properties of ΔI demonstrate, when one deals with carefully made determinations of I_2 with human subjects, in which the procedure involves or requires "mental averaging" and slow adjustment of I_2 to a best value.)

The flicker-response band in figure 1 is drawn by finding the limits of $I_m \pm k\sigma_I$. I_m is the mean intensity[6] at each fixed value of flicker-frequency F. By means of the relationship[3] between σ_I and I_m a graphically smoothed value $k\sigma_I$ is laid off from the curve through the I_m's. If an intensity I_1 is selected, we assume that the mean detectably higher intensity I_2 should be just statistically separable in its effect from the range of effects due to I_1. In practice we may take $k\sigma_I$ = P.E.I, although this does not affect the *form* of the outcome; it allows one to consider the mean higher intensity I_2 as that which would just be found discriminably higher in one half the trials. The effect, as judged by flicker frequency, just recognizable as greater than the range due to I_1 will then lie along the line ab, and will correspond to a mean intensity I_2'. $I_2' - I_1$ defines $\Delta I'$, which is necessarily proportional to $\sigma_{I'}$, and a rectilinear function of I_2'. This procedure is repeated at a number of points. It is also carried out, in exactly the same way, for the visual acuity plot (Fig. 1).

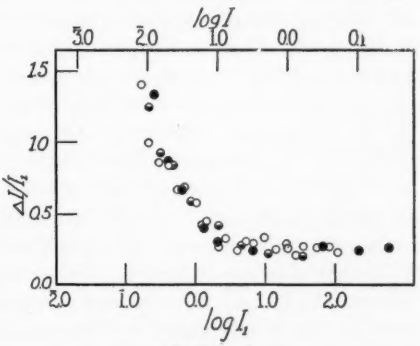

FIGURE 3

The computed ratio $\Delta I'/I_1$ (from the flicker curve in figure 1) has the same properties, as a function of I_1, as does the ratio directly measured.[4] Open and half-shaded circles, from intensity discrimination tests; solid circles, from the flicker curve; for series B^4, 0.5 unit is subtracted from log I.

The calculations may be conveniently displayed in the familiar form of $\Delta I'/I_1$ as a function of log I_1 (Fig. 2). The agreement is excellent, despite the inaccuracies of the graphic process. The result is to be compared with the directly determined values of ΔI for the same organisms.[4] In using the method of reaction to a moved background of stripes alternately illuminated by I_1 and I_2, the value of ΔI at given I_1 is also a function of the width of the stripes; the curve of $\Delta I/I_1$ *vs.* log I_1 is of the same form, merely moved to higher intensities as narrower stripes are used. The two most extensive sets of determinations have been superimposed in figure 3, and with them is shown the determinations of $\Delta I'/I_1$ from figure 2. The agreement is quantitative.

This type of analysis has been extended in several ways.[9] It depends upon the testable assumption that the reacting organism just distinguishes two intensities of an excitatory agency on the basis, essentially, of a statistical comparison of their effects. Several consequences are: (1) that ΔI is primarily an index of the dispersion of I_2, in the procedure here discussed; (2) that the properties of ΔI will differ according to the procedure used; (3) that $-\Delta I$, the just discriminable defect of intensity, will not be equal to $+\Delta I$ and will have different properties; (4) that whether the curve of $\Delta I/I_1$ goes through a minimum depends entirely upon the refinement of the procedure, even in the absence of the entry of new sensory phenomena. It is furthermore apparent that the step or increment of effect, ΔE, associated with ΔI cannot possibly be constant. The parallelism in the properties of ΔI as computed from, for example, the flicker curve, and as found directly, requires that the law of sensory intensity as a function of stimulating intensity be of the type of the flicker band $I_m \pm$ P.E.I. Hence the just recognizable increment of sensory intensity cannot be constant; it must have the properties of the vertical width of such a band.[1] This permits rational predictions of the outcome of properly designed measurements of "sensory bisection," and the construction of scales of sensory intensity.

Summary.—Recognition of the statistical character of the just detectable increment of intensity of light permits calculation of ΔI $(= I_2 - I_1)$ from suitable data upon other visual functions. The quantitative agreement between the properties of ΔI thus calculated and as determined directly requires that the law of effect (sensory intensity) as a function of stimulating intensity be dealt with as a band which measures the probability of occurrence of the index response.

[1] Crozier, W. J., *Déterminisme et variabilité*, Paris, Hermann, 56 pp. (1935); *Jour. Gen. Physiol.*, **19**, 503 (1935–36).

Crozier, W. J., Wolf, E., and Zerrahn-Wolf, G., *Jour. Gen. Physiol.*, **19**, (1935–36a) in press.

[2] Crozier, W. J., and Pincus, G., *Jour. Gen. Physiol.*, **13**, 57 (1929–30); *Ibid.*, **19** (1935–36) (in press).

[3] *Jour. Gen. Physiol.*, **19**, 503.

[4] Wolf, E., *Ibid.*, **16**, 773 (1932–33).

[5] Hecht, S., and Wolf, E., *Ibid.*, **15**, 369 (1931–32).

[6] Wolf, E., *Ibid.*, **17**, 7 (1933–34).

[7] *Ibid.*, **19**, 503.

[8] Crozier, W. J., Wolf, E., and Zerrahn-Wolf, G., *Ibid.*, **19** (1935–36a,b) (in press).

[9] Crozier, W. J., *Ibid.* (1935–36) (in press).

ON AUDITORY INTENSITY DISCRIMINATION

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A relationship presumably exists between the intensity of an excitatory agency and the magnitude of the associated effect produced in the organism stimulated. The form of this relationship is to be ascertained before a theory of the excitatory process is possible. It can be examined only in an indirect way. By "excitatory process" one necessarily means inclusively the process which determines response. If an acting intensity I produces a sensory effect E, information about E as a function of I must be based upon the discrimination of intensity I_2 from intensity I_1; neither E nor ΔE can be measured directly. The least discriminable interval, ΔI, may be most usefully obtained as $\Delta I = I_2 - I_1$, where $I_2 > I_1$, I_1 being fixed at various levels and I_2 determined by the "method of limits." The properties of ΔI have usually been examined from the standpoint of the properties of the Weber Fraction, $\Delta I/I_1$. This has not led to any very useful result.

The nature of ΔI is of special importance. Its use, notably in connection with the theory of visual excitation,[1] has been in terms of an assumption that ΔI corresponds to a fixed difference in amounts of chemical change due respectively to I_1 and to I_2, or to a constant difference in the rates of such changes.[2] The magnitudes of ΔI are essentially *average* quantities; I_2' is determined in a succession of tests, for a given I_1; the mean value of $I_2' = I_2$. A variety of cases for which adequate data exist show[3] that for visual functions of lower animals which may be measured through objective responses ΔI is consistently a simple function of I_2 (rather than of I_1); means ΔI is directly proportional to its standard deviation, and it is consistent with the properties of the relationship[3] to regard the dispersion of ΔI as determining its mean, rather than the reverse. The nature of measurements with which such examination may properly be made has been discussed elsewhere.[4] It can also be shown that with purely subjective data in which single careful determinations of I_2' are made, the (mental) averaging process is nonetheless at work in arriving at decision as to the level of I_2 and thus of ΔI, and confers upon it an identical set of properties.[5]

The question therefore arises as to whether ΔI has the same character (*a*) when suitably determined for different kinds of sense organs, and (*b*) when ΔI is obtained in such a way that it clearly depends upon a central nervous adjustor process. In the event that ΔI does exhibit essentially the same properties in these various situations, it is manifestly forbidden to assume that ΔI is to be regarded in any given case as a measure of an amount of specific peripheral chemical change (e.g., in the retina). It is, on the con-

trary, to be regarded as a statistical quantity, possessing dimensions given by the process whereby it was obtained. We are not at the moment concerned with the uses to which the statistical character of ΔI may legitimately be put.[6] It is not implied that ΔI, as a function of I_2, may not reflect a property of the peripheral sensory mechanism; but it is implied that if the peripheral and the central mechanisms concerned with the behavioral effects ("subjective" or overt) upon which the measurements rest are similar in those properties which determine σ_{I_2} and thus ΔI, then the similarity

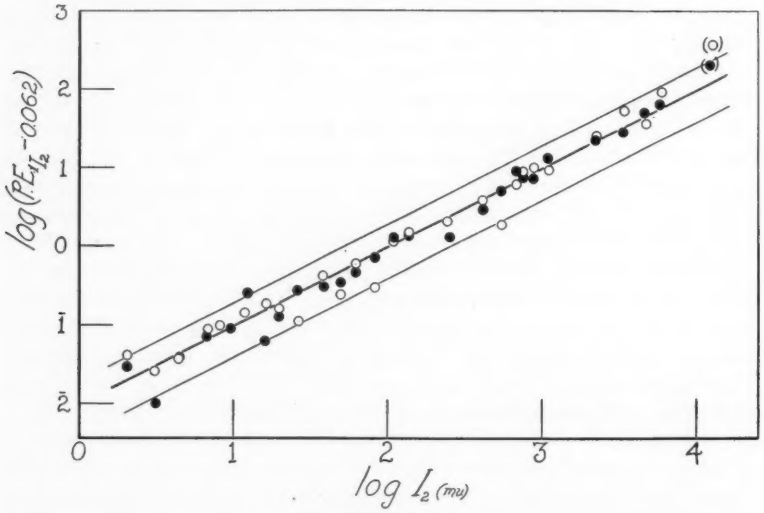

FIGURE 1

In determinations of the auditory intensity increment $\Delta I = I_2 - I_1$ required to produce just detectable change in localization of a subjectively single source of sound resulting from central fusion of effects of tones (800∼) at the two ears,[7] the dispersion of I_2, given by P.E.$_{.1I_2}$, is a rectilinear function of mean I_2. (The central line, drawn vertically half-way between the enclosing limits, has the same number of points on either side of it. The highest points, bracketed, are of doubtful value.) Open circles, I_2 for the right ear; solid circles, I_2 for the left ear.

must be due to the essentially statistical character of their modes of action in each case. It may be a long step, in such a situation, from the parameter of a statistical distribution to the velocity constant of a chemical change or to an evaluation of the number of receptor elements activated; in any case the connections between these conceptions must be ultimately clarified.

We record here the fact that in data of auditory intensity discrimination, as in the instances of visual functions already analyzed, ΔI and σ_{I_2} ($= \sigma_{\Delta I}$) are in direct proportion. The particular experiment is of added in-

terest owing to the binaural excitation employed in the method used. The procedure has been described.[7] Tones of the same frequency are introduced into each ear; the intensity of one is fixed (I_1), of the other (I_2) adjusted. The subjective experience is of a single source of ("centrally synthesized") sound located in the median plane of the subject's head.

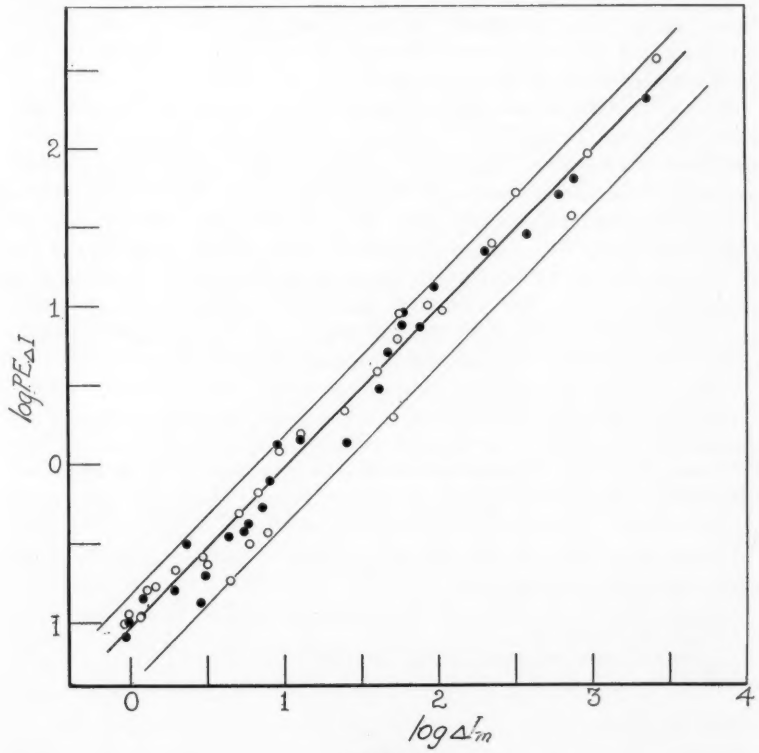

FIGURE 2

Mean ΔI is directly proportional to P.E.$_{\Delta I}$ in the data of figure 1. (The central line, drawn vertically half-way between the enclosing limits has an equal number of points on either side of it.)

When $I_2 - I_1 = \Delta I$ the apparent single source of sound just perceptibly shifts in the direction of the ear receiving I_2. The fraction $\Delta I/I_1$ as thus determined has, as a function of I_1, the usual properties of the Weber Fraction.[7]

As thus determined, also, ΔI has precisely those general properties which appear in cases depending upon the contrast of successive excitations of a

single peripheral sensory field.[3] Figure 1 shows that for these data the measure of the dispersions of I_2 (here given as P. $E._{1I_2}$) is a rectilinear function of mean I_2. In figure 2 it is demonstrated that mean ΔI is directly proportional to P. $E._{1\Delta I}$. The observations are of equal weights ($n = 10$), so that upon a logarithmic grid they should form a ribbon with parallel edges if homogeneous. If the *scatter* of I_2' really determines ΔI_m then the line of *mean* P.$E._{1\Delta I}$ should divide the plotted points into 2 symmetrical groups (Fig. 2). The line drawn through the half width of the band has 24 points on one side of it, 23 on the other.

Summary.—The mean just discriminable increment of intensity, ΔI, was established in auditory experiments based upon apparent shift of localization of a centrally synthesized sound, I_1 and I_2 originating separately at the two ears. As in visual and other tests involving successive excitation of a single peripheral sensory field, ΔI_m and P.$E._{\Delta I}$ are directly proportional, and P.$E._{\Delta I}$ is a rectilinear function of I_2. If the properties of ΔI in a given case are to be taken as due to properties of the mechanism of peripheral excitation, this can only be done to the extent that the statistical character of ΔI is recognized. Specific mechanisms of peripheral excitation cannot be based upon the data of intensity discrimination.

[1] Hecht, S., *Jour. Gen. Physiol.*, **6**, 355; **7**, 235 (1924).

[2] Hecht, S., *Jour. Gen. Physiol.*, **18**, 767 (1935); cf. also: Ebbinghaus, H., *Arch. ges. Physiol.*, **45**, 113 (1889).

[3] Crozier, W. J., *Déterminisme et variabilité*, Paris, Hermann (1935), 56 pp.; *Jour. Gen. Physiol.*, **19**, 503 (1935).

Crozier, W. J., Wolf., E., and Zerrahn-Wolf, G., *Jour. Gen. Physiol.*, **19** (1936) in press.

[4] Crozier, W. J., *Jour. Gen. Physiol.*, **19**, 503 (1935); *Proc. Nat. Acad. Sci.*, **22**, 412 (1936), cited in footnote 6 as 1936a.

[5] Crozier, W. J. (to be published in detail elsewhere) (1936b).

[6] Crozier, W. J. (1936a,b).

[7] Upton, M., *Proc. Nat. Acad. Sci.*, **22**, 409 (1936).

LIGHT GROWTH RESPONSE AND AUXIN CURVATURES OF AVENA

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1. *Introduction, Method.*—In an earlier paper in these PROCEEDINGS (Van Overbeek 1936) it was shown that decapitated Avena coleoptiles to which auxin-a was applied unilaterally, curved less if they were continuously exposed to light than if they were kept in the dark. This paper presents a closer study of the phenomenon; when the relation of time to the auxin curvatures is considered. This was possible by using a device designed by Went (in press) with which it has become possible to record the curvatures of a large number of decapitated coleoptiles at any time desired, without exposing them to light. The principal points of this method are the following. The primary leaves of etiolated seedlings were pulled out and removed and a straw from Bermuda grass (Cynodon Dactylon) about 10 cm. long, was stuck about 2–3 mm. into the lumen of the coleoptiles. A small part near the tip of these straws was photographed by a small horizontal beam of light on a revolving drum to which bromide paper was attached. In this way a record is obtained showing for each of the plants every 6 minutes the distance the straw has moved from its original position. For small angles this distance is practically proportional to the angle of curvature of the coleoptile. The curvatures of the exposed plants were recorded in a similar way. These plants were placed between two mirrors which reflected the light from a 10-watt lamp above them on two opposite sides of the coleoptiles. Between the lamp and mirrors was a water layer of about 10 cm. to check the heat radiation from the lamp. The intensity of the light striking the plants was about 500 M.C.

2. *The Light Growth Response Demonstrated by Means of Auxin Curvatures.*—Avena plants were decapitated twice with an interval of about 2 to 3 hours between them. The leaves were pulled out and the straws were stuck 2–3 mm. into the lumen of the coleoptiles. Then agar blocks containing auxin-a were applied. The auxin was extracted from cornmeal (see Van Overbeek, 1936 a and b). About 10 minutes after the blocks were put on the first recording was made. Twenty-four minutes after the blocks were put on, the light was switched on in one set of plants in order to expose them. Figure 1 shows the results of such an experiment, in which three different concentrations of auxin were used. The curve marked 1 was obtained by application of the lowest concentration, which, in the standard Avena test (Went 1935), gave a curvature of about 3°. The other

sets of curves marked 2 and 4 were obtained by application of auxin concentrations which were, respectively, 2 and 4 times as high as the one administered in set 1. The standard test of these concentrations gave 7° and 17° curvature, respectively.

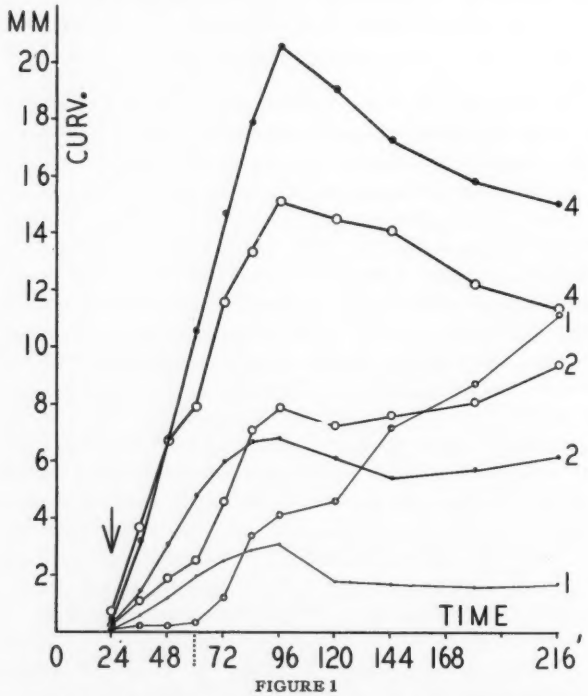

FIGURE 1

Auxin curvatures of exposed (open circles) and non-exposed (black dots) decapitated Avena coleoptiles. Abcissa: time after the block containing the auxin had been put on. Exposure to light started 24 minutes later (arrow). The vertical dotted line indicates the moment when the rate of curvature of the exposed plants begins to increase. Ordinate: curvature of the plants (in mm. deviation of the extended coleoptile from the vertical position). Mean values of 6 plants for each curve. Temperature: 20°C. Exp. number 60213.

The curves of the non-exposed plants show that the coleoptiles start to curve about 20 minutes after the blocks were put on. This is probably due to the fact that the topmost part of the coleoptile is not able to curve because the straw in that part prevents it from doing so. Then after the coleoptiles start to curve the curvature is almost directly proportional to

the time until about 72 minutes after the blocks were put on. At 96 minutes after the blocks are put on the curves start to go back. These figures have only approximate value; a detailed study of these curvatures of non-exposed coleoptiles is made by Went and is not presented here.

The curves showing the course of the curvatures of the exposed plants are quite different from the ones, just described, of the non-exposed coleoptiles. In all light-curves, but most markedly in the curves 1 and 2, two parts can be distinguished. (1) A part from the moment the exposure began until 36 minutes later, in which the rate of curvature of the exposed plants is less than in the non-exposed controls. (2) A part following the first part immediately, showing that 36 minutes after the exposure began the rate of curvature increases again. In many cases (possibly depending upon the concentration of the auxin) the rate of curvature in the second part of the curve is even higher in the light than in the dark. This is the case in the curves 1 and 2 of figure 1, and also in the two lowest concentrations of an experiment partly presented in table 1. Figure 2 shows the rates of curvature (in 0.1 mm. horizontal deviation of the straw per 12 minutes) of exposed plants as compared to non-exposed plants. This figure is calculated from the curve 2 of figure 1. Similar results are given in table 1 (column: dark-light). The horizontal dotted line in figure 2 indicates the place in the graph where the rate of curvature is the same in the dark as in the light. Below this line the rate of curvature is smaller in the light than in the dark; and above the dotted line the rate of curvature is larger in the light than in the dark.

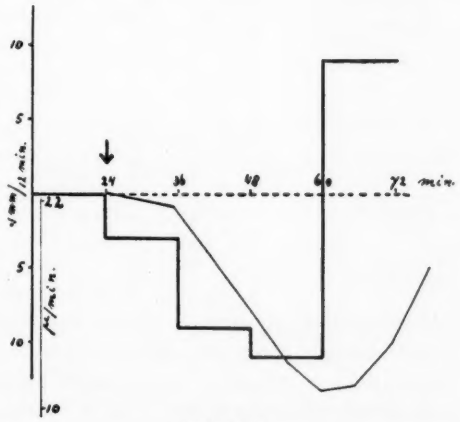

FIGURE 2

The effect of exposure to light upon the rate of curvature (heavy line) and upon the growth rate (thin line; after Koningsberger). Abcissa same as in figure 1. Ordinate: rate of curvature in the dark minus rate of curvature in the light; and (thin line) growth rate. Further explanation in text.

Table 1 shows the results of a similar experiment represented by the curves of figure 1. The relative concentration of the auxin and the curvature obtained in the standard Avena test are shown in the first column. The third and fourth columns show the increase in curvature in dark and

light during periods indicated in the second column. The fifth column shows the differences in rate of curvature between dark and light. The sixth column shows the ratio of the increase in curvature, during the first 36 minutes after the exposure to light began, of the non-exposed plants and the exposed ones (dark/light).

TABLE 1

RATES OF CURVATURE OF EXPOSED AND NON-EXPOSED AVENA COLEOPTILES. TEMPERATURE, TIME EXPOSURE STARTED, ETC., THE SAME AS IN FIGURE 1. AVERAGE VALUES OF 8 PLANTS. EXP. NUMBER 60130.

REL. AUXIN CONC.	PERIOD OF TIME	INCREASE OR DECREASE(−) IN CURVATURE DURING 18-MINUTE PERIODS DARK	LIGHT	DARK-LIGHT	DARK/LIGHT
3 (about 11°)	24–42	29	18	11	63/25 = 2.51
	42–60	34	7	24	
	60–78	20	15	5	
	78–96	21	8	13	
2 (about 7°)	24–42	22	9	11	46/13 = 3.54
	42–60	24	4	20	
	60–78	14	21	−7	
	78–96	3	12	−9	
1 (about 4°)	24–42	11	−2	13	27/−1 = ∼
	42–60	16	1	15	
	60–78	−5	21	−26	
	78–96	8	18	−10	

If the rate of curvature at various times after exposure to light as discussed above is compared with the growth rates obtained by Koningsberger (1923, p. 260, Fig. 1) on straight growing intact *Avena* seedlings a striking resemblance is noticed (Fig. 2). Koningsberger exposed the plants to 400 M.C. at 20°C. and found that the growth rate dropped until after 35 minutes a minimum was reached. From this time on the growth rate increased again.

3. *The Ratio of the Curvatures of Exposed and Non-Exposed Plants and the Influence of the Concentration of Auxin upon it.*—In an earlier paper dealing with the light growth response of Raphanus hypocotyls (Van Overbeek 1933) it was found that a definite relation exists between the ratio of the auxin curvatures in the light and the ones in the dark and the concentration of the auxin applied. When the curvatures were plotted against the concentration, then in the dark a curve was found similar to the ones described by Went (1928) and Van der Wey (1931), viz., a so-called "Blackman curve." In the light, however, the curve had an S-shape (Van Overbeek, 1933, Fig. 27, p. 604). The relation between the ratio of the auxin curvatures in light and dark and the concentration of the auxin applied was found to be a hyperbola (Fig. 28, p. 605). In a recent article by Söding (1936) it is shown for Avena that the relation between curvature and concentration of auxin can be expressed by an S-shaped curve. Söding grew his

plants and performed his experiments in the daylight in contrast with Went's method. The curvatures, below the maximum angle, obtained by Söding's method, therefore, do not indicate directly the "strength" of an auxin preparation as they do when Went's test method is used.

The light growth response of Raphanus hypocotyls consists of a decrease in growth only. The first part of the light growth response in Avena (from 24 min. to the vertical dotted line in Fig. 1) can therefore, be compared with the response of Raphanus. If for this part of the light growth response the "dark/light" value is determined, the following figures are found: For concentration 3, 2 and 1 (table 1) the dark/light ratio is 2.51, 3.54 and $\sim$, respectively. From figure 1 one can find for the concentrations 4, 2 and 1 respectively the following ratios: 1.42, 2.00 and 9.5. If these ratios are plotted against the concentration of the auxin a hyperbola is obtained (Fig. 3). This may indicate that the light growth response of Raphanus and the first part of the light growth response of Avena are of a similar nature. The increase in growth rate which is found in Avena apparently does not exist in Raphanus (see Van Overbeek, 1936b).

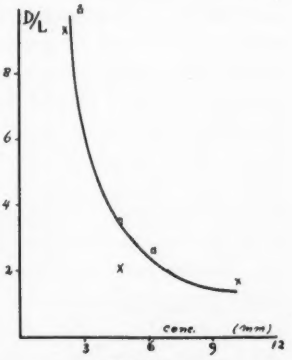

FIGURE 3

The ratio of the curvatures—36 minutes after the exposure started—of exposed and non-exposed coleoptiles as a function of the auxin concentration. Ordinate: dark/light. Abcissa: concentration. ×: obtained from experiment 60213. □: obtained from experiment 60130.

The typical increase in rate of curvature of the exposed plants to which auxin of low concentrations is applied (Fig. 1, light-curve 1) will not be considered here and is under investigation at present.

4. *Summary.*—The rate of curvature of decapitated Avena coleoptiles to which auxin is applied unilaterally shows a similar response to continuous exposure to light as the growth rate of the intact seedling does upon illumination (base growth response). The first part of the light growth response of the Avena coleoptile, which is a decrease in growth rate, is comparable to the light growth response of the Raphanus hypocotyl.

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PLANT TISSUE CULTURES FROM A HORMONE POINT OF VIEW

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A botanist, Haberlandt,[1] first pointed out the possibilities of the culture of isolated tissues. He suggested that not only could the potentialities of individual cells be determined, but that also some insight might be gained as to the reciprocal influences of tissues upon one another, that is, as to "correlation." Haberlandt's many experiments with plant cells did not succeed. Harrison, Burrows and Carrel, using animal tissue, were able to realize Haberlandt's ideal, and from the more recent work of Fischer, Ephrussi, Gaillard and Chambers, it is evident that many different kinds of problems can be attacked by the method of tissue culture. Since the time of Haberlandt there have been repeated attempts to cultivate plant tissue in artificial media, or at least *in vitro*. Embryonic tissue has been grown under many conditions. Thus Hannig[2] grew immature embryos in artificial media and eventually raised mature plants from them. LaRue[3] has recently cultivated fragments of embryos and has obtained mature plants from such fragments. It should be clear, however, that the concept of "tissue culture" does not embrace such experiments. The embryos of Hannig and others have always differentiated into more or less normal complexes of tissue even though grown on artificial media. The embryonic fragments of LaRue have similarly differentiated, and are, in fact, typical examples of "regeneration" in the sense of Loeb. Isolated root tips were first cultivated *in vitro* by Robbins[4] and by Kotte,[5] but to White[6] is due the credit for having worked out the cultural conditions capable of sustaining the indefinite growth of these organs. In this case again, as is well shown in the recent work of Robbins, Bartley and White,[7] the root meristem continues to differentiate in a comparatively normal fashion. Cultures of the various component tissue of the root have not as yet been possible. In fact, cultivation of isolated plant tissue has been accomplished only by Schmucker[8] with palisade cells, but his results cannot as yet be confirmed.

This signal lack of success in the cultivation of isolated plant tissues is undoubtedly in part due to the use of unsuitable tissue. On the other hand it is also certainly due in part to unsuitability of the media employed. Because of the work on auxin we are now beginning to realize the great part special chemical substances or "hormones" play in plant growth and development, and it seems probable that such substances must be present in any medium in which plant tissue is to be successfully cultivated. We cannot, however, supply these substances as simply to plant cultures as to

animal, since they are not readily available in embryonic extract. Experience has shown that extract of plant embryos is in general without effect or actually toxic for the growth of excised plant tissue. White has shown, however, that there is a substance (or substances) present in minute amounts in yeast which is essential for the continued growth of excised roots. That analogous substances are necessary for the growth of other organs and tissues, and that these substances may also be derived from outside sources, seems a fair inference. The objectives of the present work have therefore been the separation and purification of special substances or hormones which control growth and development of plant tissues and organs, and the perfection with the aid of such substances of true *tissue cultures*. Only a portion of this work will be reported here, and the remainder will be discussed in greater detail elsewhere.

If a young string-bean pod be split lengthwise along the sutures and the immature seeds removed, a series of "cups" lined with small iso-diametric parenchymous cells is exposed. The parenchymous lining of the cup is very sensitive to injury and responds to a prick by a hypertrophic outgrowth of dividing and enlarging cells. A similar but larger outgrowth follows in response to certain tissue extracts, as first described by Wehnelt.[9] If small drops of water are placed in the tissue cup no reaction occurs.[10] Similarly, auxin is without effect except in concentrations sufficiently high to be toxic, when a small reaction occurs (see also Jost[11]). Tissue extracts, however, either of the bean or of other plant organs, particularly green parts, cause a "wart" like protuberance of the parenchymous tissue. This outgrowth is limited to the area directly under the drop of tissue extract, and may be as much as 1.5 mm. high. Cross-sections of the wart show that it consists of cells elongated at right angles to the surface of the cup. Cell divisions may also be found (see Jost[11]), their number depending on the variety of bean used. Thus golden wax and valentine varieties gave no cell divisions, Kentucky wonder number 1 gave a few, and Kentucky wonder number 2 gave many cell divisions.

Standard conditions for the "bean test" have been established, and it has been possible to perform semi-quantitative tests for the factor (or factors) in question by determination of the dilution in which a given preparation is just active. In this way the activity of a solution may be estimated to about ± 3 times. The following chemical properties of the factor involved, a few of which were previously reported by Wehnelt, have been established:

1. Soluble in water, 75% alcohol.
2. Insoluble in ether, chloroform, butyl alcohol, absolute alcohol.
3. Stable to H_2O_2 in both acid and alkaline solution.
4. Relatively heat stable in both acid and alkaline solution.
5. Adsorbable from water by charcoal, elutable in 75% alcohol.

6. Precipitatable by alkaloidal reagents (phosphotungstic acid, picric acid).

A partial purification of the factor is possible on the basis of the properties enumerated above, and this purification is being continued. It would be of interest to know whether or not the bean reaction is due to one factor influencing both cell division and cell elongation, or to two or more separate substances. With this in view, pantothenic acid, a "growth hormone" for certain strains of yeast, and kindly supplied by Prof. Roger Williams, was tried in the bean test. It was completely without activity over a wide range of concentrations. Similarly vitamines B_1 and B_2, shown by Schopfer[12] to be growth substances of Phycomyces, do not come in question here since they have chemical properties different from those enumerated above. The conclusion of Dagys[13] that the growth hormones of the lower and the higher plants are closely related would seem open to some question. One may also draw the conclusion that the auxins are not the only cell elongation hormones of the higher plants, since we have here cell elongation due to a substance of quite a different type (insoluble in ether and chloroform).

The fact that the parenchymous cells of the bean pod respond actively to this extract *in vivo* suggests that such cells might be suitable for cultivation *in vitro*. Accordingly a large number of experiments on their cultivation in liquid media have been made. Of the various solutions, used as a base for the medium, the best thus far has been found to be a somewhat modified White's[6] solution; although this is in all probability not optimal. The solution was made up as follows:

$Ca(NO_3)_2$	230 mg.	KH_2PO_4	12 mg.
$MgSO_4$	35 mg.	$Fe_2(SO_4)_3$	2 mg.
KNO_3	80 mg.	sucrose	20 gm.
KCl	65 mg.	water	1 liter

Tissue extract for the experiments reported here were made by extracting 250 gm. of fresh beans with 250 cc. of 75% alcohol for 8 hours, evaporation of the alcohol, filtering and dilution of the filtrate to a total volume of 200 cc. This extract was then diluted with an equal volume of the above culture solutions which had been made up to twice the final concentration.

Cubic pieces of tissue approximately 1 mm. on each side were removed under sterile conditions from bean pods and placed in petri dishes with 10 cc. of the above medium. The petri dishes were then left in the dark for 6 days. At the end of this period control cultures to which no extract had been added showed no growth whatsoever. If bean extract had been added a very striking growth of the parenchymous tissue took place; in some experiments an increase of volume of as much as 40 times. The originally cubical tissue fragment rounded out as it enlarged and assumed a spherical shape. The enlargement depended, in the main, upon elongation of the peripheral cells. At the base of this zone of greatly elongated cells was found

a "meristematic" zone, particularly in cultures of Kentucky wonder number 2. Superficially these cultures resembled strikingly the cultures of fibroblasts *in vitro*. In reality, of course, the cells at the periphery were "migrating" only by their growth and not by any independent active movement.

At the end of six days new fragments approximately 1 mm. on each side were cut from the central portion of the original cultures and placed in fresh medium. These "subcultures" grew as did the original cultures. Subcultures were continued, each time fragments being taken from the center of the old culture. After the first two cultures, however, the growth steadily declined until it became practically 0, as is shown in table 1.

TABLE 1

No. of subculture	0	1	2	3	4	5	6	7
Av. diam., mm.	1	4.5 ± 0.6	4.5 ± 0.7	3.3 ± 0.3	2.8 ± 0.3	1.8 ± 0.3	1.5 ± 0.3	1.3 ± 0.2

It was at first supposed that this decline might be due to the exhaustion of some other essential factor originally present in the tissue. The addition of other substances to the later cultures, as well as to the culture during its entire history, was therefore attempted. Peptone, yeast extract, heteroauxin and malt extract were tried in this way, each over a considerable range of concentrations, but no substantial improvement of the later cultures was found. It seems more likely that there is a cumulative toxic effect of the crude preparation employed, but a test of this hypothesis must await further purification of the active principle.

The chief interest of the cultures described here is that they represent a somewhat closer approach to true plant *tissue* cultures than do other attempts thus far reported, even though they are not, as yet, capable of indefinite subculture. They show, in the first place, both cell division and cell enlargement, and not merely cell enlargement as did the cultures of Haberlandt, Bobilioff-Preisser[14] and others. In the second place, parenchymous tissue in this case continues to grow as parenchymous tissue, and there is no differentiation into root and shoot as in the cultures of LaRue, or into vascular tissue as in the root cultures of White. It is necessary to note, however, that the present cultures are not completely without a progressive differentiation, since the greatly enlarged cells of the periphery are incapable of further division, and subcultures must be made from the central portion of smaller, dividing cells.

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'INHIBITION OF REINFORCEMENT' AND PHENOMENA OF EXPERIMENTAL EXTINCTION

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In the literature on conditioned reflexes, two contrasted varieties of curves of experimental extinction have been described. The first type, illustrated in the experiments of Pavlov,[1] Kleitman and Crisler,[2] Switzer[3] and others, is characterized by a continuous decline in the magnitude of the conditioned response on successive unreinforced elicitations. The decline is rapid at first, then more and more gradual. The second type, reported by Switzer,[4] Scott,[5] Hudgins[6] and Hilgard and Marquis,[7] shows a larger response on the second or third extinction trial than on the first, demonstrating the initial rise characteristic of these curves. Hull,[8] in his summary of studies of conditioned reflexes, points out that "as yet the experimental conditions which bring about these two types of curve have not been determined" (p. 438).

The initial rise in the extinction curves of the second variety has been attributed to a "practice effect" or "improvement through use." This fails to explain why the rise is not uniformly observed. Research by the writer[9] on the irradiation of conditioned responses has suggested an explanation based upon the experimental conditions of the reinforcement process. There appears to be a negative adaptation to continuous reinforcement, an effect which may be labeled, for descriptive purposes, the 'inhibition of reinforcement.'[10] Following protracted reinforcement the omission of the unconditioned stimulus might be expected to produce 'disinhibition,' resulting in an augmentation of response on the second or third extinction trial. This explanation for the rise in their extinction curves has been recently proposed by Hilgard and Marquis:[7] "The first extinction trial is followed by altered conditions. . . This unexpected

omission may act as a disinhibitor, and result in a larger response. . . on the second trial" (p. 48).

The proposed hypothesis of 'inhibition of reinforcement,' in conjunction with other recognized conditioned response principles, would lead to the following deductions: (1) 'Inhibition of reinforcement' should increase with an increase in the number of massed reinforcements. An initial rise in the curve of extinction should consequently be expected only when a considerable number of massed reinforcements have produced 'in-

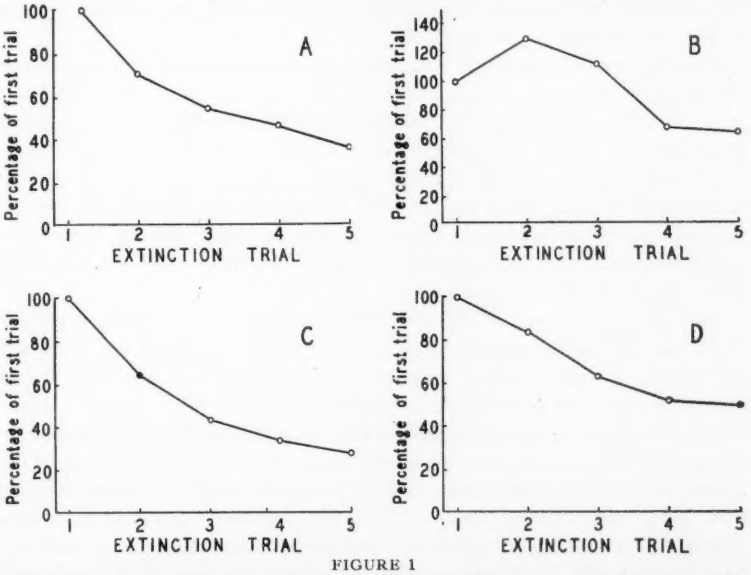

FIGURE 1

Extinction curves following various conditions of reinforcement. Results plotted in terms of ratios (in per cent) of responses on successive extinction trials to response on first extinction trial. (*A*) 8 reinforcements. Extinction immediately. (*B*) 24 reinforcements. Extinction immediately. (*C*) 24 reinforcements, distributed into 3 groups of 8 each. Rest period of 30 min. between groups. Extinction immediately after last group of reinforcements. (*D*) 24 reinforcements. Extinction 30 min. after last reinforcement.

hibition' in sufficient quantity to make possible 'disinhibition.' Some experimental evidence for the validity of this deduction is afforded by Wenger's observations that more 'inhibition' is manifested after twenty-five than after twenty reinforcements. (2) When reinforcements are distributed over a long period of time the 'inhibition of reinforcement' should be dissipated between successive reinforcements, and hence no initial rise in the extinction curve due to 'disinhibition' should be produced. This deduction is in accord with the statement of Pavlov[1] that "one and the

same stimulus which is constantly reinforced and repeated many times at long intervals of time loses only little of its effect: the same stimulus when applied at short intervals of time quickly diminishes in its effect" (p. 248). (3) Similarly, if a period of time is allowed to elapse between conditioning and extinction, the 'inhibitory' process, declining more rapidly than the 'excitatory' [cf. Pavlov,[11] "... the process of internal inhibition is more labile (unstable) than that of stimulation" (p. 138); Pavlov,[1] pp. 58 ff. and 99; and Hull,[12] p. 503], should be dissipated; consequently no 'disinhibition,' producing an initial rise in the curve of extinction, should be anticipated.

The experimental procedure used to test the above deductions was the following: The response conditioned was the galvanic skin reaction. The Burr-Lane[13] vacuum-tube electrometer was employed for measuring potential changes independently of resistance variations. An electric shock produced by an inductorium was the unconditioned stimulus. The conditioned stimulus was a tone of 1000 cycles, 40 decibels above the threshold, produced by a beat-frequency oscillator. The stimuli were presented automatically; the tone was sounded for 400 ms. and was followed, after a pause of 100 ms., by the shock.

Four groups, of twenty subjects each, were equated on the basis of galvanic response to the unconditioned stimulus before conditioning. Group I was given 8 reinforcements. Extinction was started immediately after conditioning. The subjects in Group II were given three times as many reinforcements; extinction was likewise begun immediately after reinforcement. Group III was given the same number of reinforcements as Group II but 30 minutes were allowed to elapse between reinforcements and extinction. Twenty-four reinforcements were likewise given to Group IV, but they were divided into three groups of eight reinforcements each, separated by 30 minute intervals. Extinction was begun immediately after the termination of the last group of reinforcements. In all cases the reinforcements and extinction trials were given at approximately one-minute intervals, varied slightly to prevent temporal conditioning.

The results, presented in the accompanying figure, are in accord with the deductions, and thus constitute confirmatory evidence for the hypothesis of 'inhibition of reinforcement.' When few reinforcements are given a continuous fall in the extinction curve results (*A*). With a much larger number of reinforcements, however, the curve manifests an initial rise (*B*), in harmony with the theoretical expectation. When the reinforcements are distributed (*C*), or when time is allowed to elapse between reinforcements and extinction (*D*), no initial rise is obtained. Statistical procedures show the results to be reliable, and over 90% of the individual curves follow the pattern of the group average for the particular experimental procedure employed.

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DEMONSTRATION OF A HATCHING SECRETION IN RANA PIPIENS SCHREBER

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Kerr,[1] studying *Lepidosiren*, was apparently the first to suggest the action of a capsule digesting ferment as a means of releasing the larva from the egg membranes. Wintrebert,[2] and Noble and Brady[3,4] reported secretion concerned with the hatching of certain Urodeles. Of the Anura, *Xenopus*,[5] *Hyla*[6] and *Alytes*[7,8] have been studied. As with the Urodele experiments, the observations suggest that a digestive secretion is liberated by the embryo during the hatching period. Nevertheless, the evidence so adduced does not seem conclusive to the present writer. References to the literature of hatching enzymes may be found in the work of Needham.[9]

The jellies and vitelline membranes of early tail-bud larvae of *Rana pipiens* were removed with iridectomy scissors. Covered stender dishes each containing from 100 to 350 of such freed embryos in 10 cc. of Great Bear Spring water or distilled water, were placed in an incubator maintained at 23°C. Along with this series were included dishes containing a number of normally enveloped embryos of the same stage to serve as indicators of the close of the hatching period. Several hours after all of the latter had hatched, the contents of the stender dishes in which the freed embryos had passed the hatching period were filtered, the filtrate centrifuged and decanted.

It was found that such preparations removed the jellies from fertilized

eggs, blastulae, gastrulae and neurulae immersed in them. In all cases the vitelline membrane was affected, either markedly swelling away from the egg or actually rupturing. Where the egg had not been released, the vitelline membrane could easily be pulled from it. The vitelline membranes failed to undergo solution, although the small amounts of fluid used were sufficient to dissolve the jelly completely.

Individuals were freed from their jellies in from one to several hours at room temperature, the rate depending upon the initial number of embryos used to prepare a given volume of the filtrate, the volume used per egg and the stage of development of the egg. In general, earlier stages were released more slowly than later stages by all preparations. (Dr. M. Atlas, of this laboratory, states that the fluid obtained from 400 membraneless embryos of *Rana pipiens* in 2 cc. of Great Bear Spring water removed the jelly from early and late neurulae within a quarter of an hour, from cleavage stages in half an hour.) Thus solutions of the secretion allowed easy removal of the membranes from the eggs of *Rana pipiens* at stages when manipulative procedures were both difficult and likely to injure them. Eggs and embryos so released were found to develop quite normally after transference to Great Bear Spring water.

The filtrates were found to be thermo-labile, being inactive after boiling. Standing, even at lowered temperatures, caused clouding and loss of activity within two or three days. Fluids which were recovered after successful artificial hatching and then refiltered, evinced little or no capacity for further action. Great Bear Spring water in which large clutches of eggs had hatched normally seemed similarly inactive.

The experiments show clearly that something is liberated from the embryo at the time of hatching which dissolves the jelly and affects the vitelline membrane.

I am deeply indebted to Professor L. G. Barth, in whose laboratory these experiments were carried out.

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[2] Wintrebert, P., *Compt. Rend. Assoc. Anat.*, **23,** 500 (1928).
[3] Noble, G. K., and Brady, M. K., *Anat. Rec.*, **45,** 274 (1930).
[4] Noble, G. K., and Brady, M. K., *Zoologica*, **11,** 127 (1933).
[5] Bles, E. J., *Trans. Roy. Soc. Edin.*, **41,** 807 (1905).
[6] Bles, E. J., *Ibid.*, **41,** 809 (footnote) (1905).
[7] Noble, G. K., *Amer. Mus. Nov.*, **229,** 1 (1926).
[8] Bergeot, P., and Wintrebert, P., *Compt. Rend. Soc. Biol.*, **95,** 1329 (1926).
[9] Needham, J., *Chemical Embryology*, 3 vols., Cambridge (1931).